GROWTH AND DEVELOPMENT OF SHEEP

IN RELATION TO FEEDING STRATEGY

by

Mark Rowan Cropper

A thesis submitted towards the degree

of Doctor of Philosophy

UNIVERSITY OF EDINBURGH

September 1987

DECLARATION

This thesis has been written by myself. The experimental work was conducted with the assistance of members of the Edinburgh School of Agriculture. The results and analyses, which have not previously been submitted for any other degree or qualification, were carried out by myself.

Mark Rowan Cropper

17 September 1987

ABSTRACT

The results of five experiments are reported as tests of a theory of the growth and feed intake of sheep. An attempt is first made to describe potential growth in the sheep, that is, growth under non-limiting conditions, and to generalise this description across breeds. The two ways of providing non-limiting conditions are then considered. This approach necessarily confronts the problem of predicting the desired intake of feed resources required to fulfill the potential. Whilst ad libitum access to a single, nutrient-rich feed is found an acceptable method, data collected in three experiments, using a total of 64 Suffolk X Greyface lambs, lead to the conclusion that sheep can also attain their potential for growth when given free and continual access to more than one feed, a possible combination of which is non-limiting to growth. It is suggested that the technique may be applied as an independent test of other estimates of resource requirements for growth and to the prediction of feeding behaviour in sheep. The responses of sheep to limiting conditions for growth are studied on the assumption that sheep have rules for partitioning the feed's first limiting resource. The limits to this view are investigated by experiment using 73 Scottish Blackface wethers offered amounts of feed which provide similar crude protein allowances but different yields of energy. It is concluded that the body composition of sheep can be manipulated by nutrition, since the animals will partition scarce energy resources to protein growth before fattening, but that this effect is complicated in ruminants because protein supply is not independent of feeding level. The theory is then applied to the problem of predicting the recovery of sheep from the effects of growth restraint. An experiment involving 30 Scottish Blackface wethers provides data which support the idea that sheep, following a period of underfeeding, will resume their known potential for growth and, only when necessary, restore their body composition to the state dictated by their inheritance. No compensatory growth is observed. Finally, the work as a whole is discussed in relation to animal science and the sheepmeat industry. Possibilities for future research are also suggested. The experimental data are published in full in the appendices.

ACKNOWLEDGEMENTS

The author's thanks and acknowledgements are due to the offices of the Ministry of Agriculture, Fisheries and Food and the Edinburgh School of Agriculture for their cooperation in the funding of this work.

To my supervisor Mary Lloyd for her efforts in initiating the project and for criticising my approach to the subject.

To my supervisor Charlie Hinks for overseeing my studies.

To members of the Edinburgh School of Agriculture for their support and assistance in the practical work:

Jack FitzSimons
Hazel Brown
Jim Fraser
Tom Dick
Dave Anderson
Terry McHale
Willy Wood
Tom Beasley
The staff at C.A.L.

To Pat Phillips for statistical advice and Sandra Gray for typing the tables.

To Billy Z. for, amongst other things, typing everything else except the acknowledgements.

To my friends Chas.Wall, Ilias, Bill D., Dave, Margaret, Peter and Eva for services beyond the normal call of duty.

To Costas Stamataris for teaching me how to run an experiment.

To Gerry Emmans for patiently introducing me to many rich and fruitful ideas and for always expecting me to do better.

TABLE OF CONTENTS

PREFACE

A scientific approach to the study of sheep has been adopted by agriculturalists since the foundations of the subject were laid by Lawes and Gilbert in the 1850s.

> To the Farmer who is engaged in producing animal food for the consumption of the community at large, it is very desirable to know...what is the probable proportion of the consumed food, or of its several constituents, which he recovers in the form of meat? --how much he may calculate as manure? --and how much as expenditure or loss by the feeding process? Lawes and Gilbert (1859).

Seventy years later, in response to a changed economic climate, Hammond engaged the Cambridge School in further analysis of the sheep as, primarily, a producer of food. Under current farming conditions, research into the growth of sheep is still motivated by the need to predict the performance of a lamb in terms of its yield of meat.

Croston and Pollott (1985) have suggested that research into the physical and financial bases of sheep production remains important if the sheep industry is to stay profitable despite the declining consumption of sheepmeat and increasing reliance on EEC subsidy. Prescott (1981) attributed the decreasing popularity of lamb to its high price relative to pork and chicken and its seasonal variability in supply. Kempster (1981) added that sheep producers and traders had been slow to respond to the changing consumer demand for less fatty and more convenient meat products.

However, Croston and Pollott (1985) did emphasise the problems that sheep farmers face in providing carcasses of the fatness and weight which meets the requirements of a given market outlet. They argued that the number of kinds of sheep (cited as 56 pedigree and 300 crossbred types in the UK) and the range of environments in which they are reared, makes planned sheep production difficult because farmers do not have sufficient information about their production system on which to base their management decisions.

The ideas and experiments presented in this thesis are directed towards obtaining a reliable description of both the growth potential of a given sheep type and the conditions under which ideal growth may be achieved. The

responses of sheep to (a) conditions which are limiting to growth and (b) the restoration of non-limiting conditions after a period of underfeeding, are then addressed. Finally, the implications of the work to the prediction of lamb performance are discussed in relation to feeding system and the quality of the lamb product.

CHAPTER 1
THE POTENTIAL FOR GROWTH IN SHEEP

1.1 The Genotype as a Determinative Inheritance

The view that a growing lamb is a living, organic whole accords with Aristotle's idea of organisms as the 'telos or final cause of their own generation and development' (Thompson, 1917) which finds its modern counterpart in the concept of the genotype. Here, the genotype of the individual is taken to represent, in part, a determinative inheritance; that is, a growth-plan or principle of ontogenesis that directs what, at conception, is still a potential for actual growth. This means that the capacity to grow is treated first as an idea and, subsequently, that the way the lamb actually grows in an ideal environment is a reflection of the inherent potential for growth. This view presumes that ideal or non-limiting conditions for growth can be found and that the animal is able to make full use of them. Since, according to Darwin's theory of evolution, it is the genotype of 'successful' or 'fit' parents which has been transmitted successively to the offspring and has provided them with all that they need to take advantage of the prevailing conditions of the environment, part of the genotype is also held to bestow on the animal a means by which it may fulfill its potential. These aspects of the inheritance and the environment will be considered in Chapter II.

In the meantime, the term 'potential growth' will be used in the sense of 'measured growth under non-limiting conditions' and, therefore, in the empirical approach to growth adopted in this thesis, a description of the quantitative changes in form (development), into which the inheritance will direct the animal, is required. For such purposes, the inheritance of the animal is taken to motivate the animal to attain:

a) the mature form of a fully reproductive (fit) individual.

b) the maximum (desired) rate at which form may be changed up to the mature equilibrium (Eckles and Swett, 1918; Blaxter, 1950).

in compliance with the idea that the most successful animal is that which reaches full fecundity at maturity in the shortest period of time i.e. its success

is based on an optimising strategy, (Krebs and McCleery, 1984).

The definition of growth thus becomes simply one of a progress towards a mature end-point (Courtis, 1937).

1.1.1 The Measurement of Growth

Lawes and Gilbert (1859) relied chiefly on the measurement of liveweight in their investigations [1] but they recognised that liveweight records alone are a poor way to define growth since differences may arise which cannot be regarded as true progress to maturity, the least predictable being the weight of gut contents and the dampness or dirtiness of the fleece. Nevertheless, liveweight measurement had the advantage of being straightforward to make and repeatable on an individual.

Later workers, led by Waters (1908), turned to linear measurement of the animal as their best, repeatable indicator of growth. Though some of these data e.g. girth diameter were found to share the same failings as liveweight in that they reflect, primarily, differences in gut-fill, other measurements such as height at the withers were far superior (see Chap. III), indicating growth of the skeleton when liveweight was static or falling.

However, Waters belonged to a tradition of workers (reviewed by Armsby, 1908) who knew that, convenient as they were, linear and anatomical measurements could not be applied sensibly to matters of nutrition. Since the earliest days of nutrition science, scientists had seen the need for a common chemical scale on which to measure both the feed offered and the growth made. The relationship between the measures of liveweight, linear and chemical growth were discussed in the monograph of Armsby and Moulton (1925). In that work, the authors emphasise the relevance of defining progress to maturity as a gain in the lipid-free empty body, that is, on the 'protoplasmic basis' of Greene (1919). The advantages of this system were praised by Murray (1919) since

> The composition of the non-fatty matter is practically constant.

[1] though, it must be added, they also made the advanced observation that the composition of the gain was critical to the yield of animal products and the efficiency with which liveweight was gained.

> It is the same in cattle, sheep and pigs and is not affected by condition but varies slightly with age.

and it reemerged in a modified form (as the fat-free empty body) in the argument of Elsley, McDonald and Fowler (1964) who tried to settle the debate between Wallace (1948) and McMeekan (1940) in the interpretation of the growth of pigs.

In this thesis, growth will be taken, where possible, as an increase in the weight of protein in the animal. Though a reversible process under starvation conditions, increase in protein weight is considered to be the best indicator of progress towards maturity because protein is primarily a structural component in the body and has a direct relationship to the metabolic processes of the animal (Schmidt-Nielsen, 1984). In the absence of chemical composition data, muscle weight will be taken as the most closely related quantity to protein weight, whilst recognising the errors associated with unmeasured quantities of intramuscular fat.

Section 1.1.2. will consider how the coordinated change in form (development) of the lamb, as it grows under non-limiting conditions, can be reduced to simple mathematical descriptions by tracing the relative growth of each component of the body against the protein baseline, for chemical constituents, or the muscle baseline for anatomical parts. Functions for describing the rate at which the protein and muscle weight increase during potential growth are then appraised in section 1.1.3, and the two equation types are synthesised to make statements about the growth which the whole animal should attain if it is to fulfill its potential (section 1.2).

1.1.2 The Allometry of Development

Within the concept of the fitness of a genotype it is implicit that the change in form that the growing individual undergoes must also keep the immature animal in a continuous state of adaptation, or harmony, in relation to the environment (p.580,Ch.17: Brody, 1945).

The physical manifestation of the harmony as a differential growth of the parts of the body in the maturing animal was a chief interest of Thompson (1917) who inspired Huxley (1932) to formulate an algebraic method (allometry) for describing the changes in animal form. The now familiar relation is most

commonly given as

$$Y = a.X^b \qquad (1)$$

which may be written

$$\ln Y = (\ln a) + b\,(\ln X) \qquad (2)$$

where ln is the natural logarithm of a value, X and Y are the weights of two related parts of the body, a is the intercept and b the slope or growth coefficient, both of which are constant for a given part in a given genotype.

The allometric equation has been widely applied in the analysis of body composition data of both pre- and post-natal animals [2] as a means of making linear those relationships between parts which would otherwise be curvilinear and hence difficult to compare mathematically. In this respect, the procedure has great advantages (p.398, Ch.13: Brody, 1945) but is weakened in those cases where

a) the equation has been fitted between two components (e.g. between gut-fill or gut, and liveweight) when allometry was a poor description of the data.

b) a part of the animal (y) has been related to the whole (x), a technique which is mathematically unsound since the equation relies on the two variables being independent.

The allometric equation is used in this review to provide a simple, mathematical description of the direction in which the inheritance of the animal guides the change in form (development). The derived allometric equations then give an expectation of the form that the animal should have (i.e. the desired form at any given degree of maturity, u) and this expectation is subsequently used to determine the effect of limiting conditions on the development of the animal.

In this thesis a component of the body is nominated as the independent variable (x) against which each other component, (y), is plotted. The muscle weight of the cold carcase (M_t) has been chosen as the independent variable

[2] These may be found summarised in ARC (1984), Chap. I.

for anatomical relationships. This procedure resembled that recommended by Jackson (1967) who related carcase muscle to a baseline weight of carcase bone. Protein weight of the empty-body (P_t) is used in chemical descriptions of growth.

1.1.2.1 The Allometry of Anatomical Components in the Body

The greater part of the published data, in which part-whole relations have been studied do not provide the actual data for deriving the allometric coefficients for sheep by the part-part method.

However, the studies of Lloyd, Emmans and Prescott (1985) on the growth of Scottish Blackface (SBF) wethers under non-limiting conditions [3] supplied body composition data for allometric analysis from lambs of muscle weight 3.6 kg ($\bar{0.22}$) to maturity (average = 16.5kg). The relationships derived from these data were to have the additional convenience of providing expectations of potential post-natal growth of the same lamb-types employed in subsequent experiments over similar degrees of maturity.

The low residual standard deviations reported in Table 1.1 show that the analysis gave a good description of the relative growth of the head, bone, pluck (lungs + heart) and pelt (fleece + skin) components. However, the large number and wide spread of the lamb's weights caused the relation between fat depots and muscle weight to be highly significant but very variable. In their comments on the fattening characteristics of sheep, Butterfield, Griffiths, Thompson, Zamora and James (1983) suggested that it is difficult to tell whether such variability, which has also been found by previous workers , is due to inherent genetic variation or to unmeasured environmental effects. A possible solution to this problem, which was attempted in the experiment of Lloyd *et al* (1985), is to find the best way of ensuring that lambs receive non-limiting conditions for growth under which they can express their true, genetic potential to fatten. The growth of fat and bone relative to muscle is presented graphically in Fig. 1.1., using the data of Lloyd *et al* (1985).

It is a feature of allometric analysis that body components with a

[3] For a description of non-limiting conditions and a justification for using these data see Chap. II.

Table 1.1 Allometric Growth Coefficients of the Anatomical Components of Scottish Blackface lambs (n=32) given non-limiting conditions for growth

Component (y)*	Growth coefficient (b)	Residual standard deviation	Equation
Head (with horns)	0.67	0.097	A
Bone (excluding head and feet)	0.69	0.085	B
Liver	0.76	0.145	C
Pluck (lungs and heart)	0.83	0.124	D
Pelt (skin and fleece)	1.26	0.149	E
Intermuscular fat (IMF)	1.88	0.281	F
Total carcase fat (TF)	2.34	0.305	G
Subcutaneous fat (SCF)	2.74	0.373	H
Kidney knob and channel fat (KKCF)	3.04	0.401	I
Caul fat (CF)	3.70	0.564	J

* analysis in the form $y=a(muscle)^b$, using the data of Lloyd *et al* (1985)

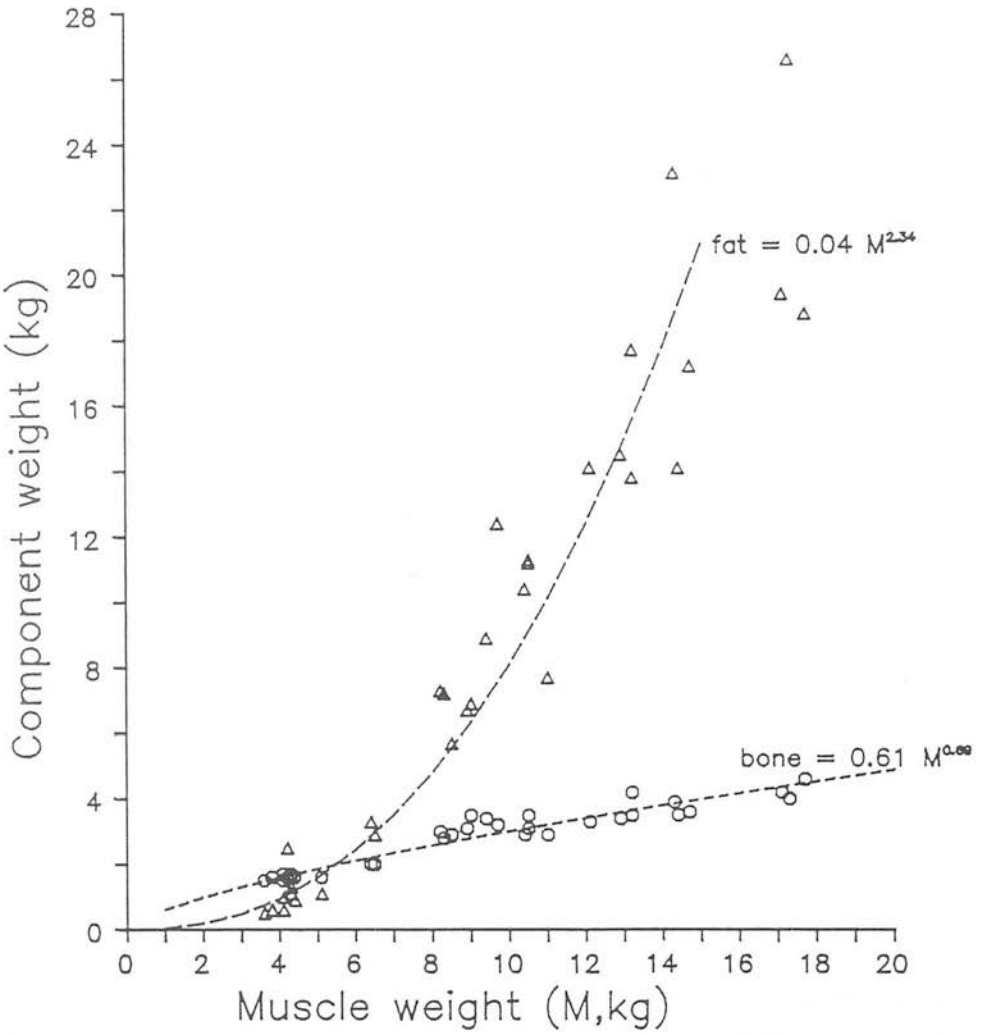


Fig. 1.1 The Relative Growth of Anatomical Components in Scottish Blackface wethers (n=32) under non-limiting conditions

regression coefficient less than 1.0 reach their maximum rate of potential growth earlier than the independent variable, in this case, muscle. Such components are conventionally called 'early maturing'. Conversely, the later maturing components have b values greater than 1.0. Hence, Table 1.1 indicates the progressive development of the post-natal lamb's body components beginning with early maturing of the head (including brain) and skeleton, followed by the vital organs (pluck and liver) through to the late-maturing reserves of fat. The sequence of development will be considered further in relation to rates of growth in section 1.2.2.

It will be noted that the organs of the alimentary tract (gut) and their contents have been omitted from the allometric analysis in Table 1.1. The reason for this is that both these components have been known not to increase in an allometric relation to muscle or liveweight (Hammond, 1932). The size and nature of the gut of ruminants, particularly the reticulo-rumen, have been shown to be dependent on the type of feed offered to the animal. Wilckens (1865) was aware that rumen development was retarded if the young ruminant remained exclusively milk-fed. Wardrop (1960) summarising the findings of many workers said that solid feed, especially roughage, must be available after three weeks of age if the forestomachs of the lamb are to develop adequately. Attempts have been made to relate in other species the gutsize to both degree of maturity and the rate of feed intake (Kirkwood and Prescott, 1984) and this would appear to be a promising approach to the problem. The prediction of the weight of gut-fill from a knowledge of the rate of feed intake (and presumably water intake too) and the composition of the feed has been suggested by ARC (1984) and Emmans and Fisher (1986).

Fig. 1.2 shows that an allometric relationship could not be fitted to the gut data of Lloyd *et al* (1985) because of a decline in the weight of the component beyond 9kg muscle weight. In addition, the simple relation between gut-fill and muscle was regarded as fortuitous, in this instance, and so quadratic functions were fitted to both data sets for the purposes of summarising their gains relative to muscle growth.

Therefore, the majority of the sheep's anatomical body components have been related simply and successfully to the increase in weight of muscle as the animal grows and allometry has provided an adequate and helpful description of the anatomical form that the animal should have (that is, its desired form) at any given degree of maturity.

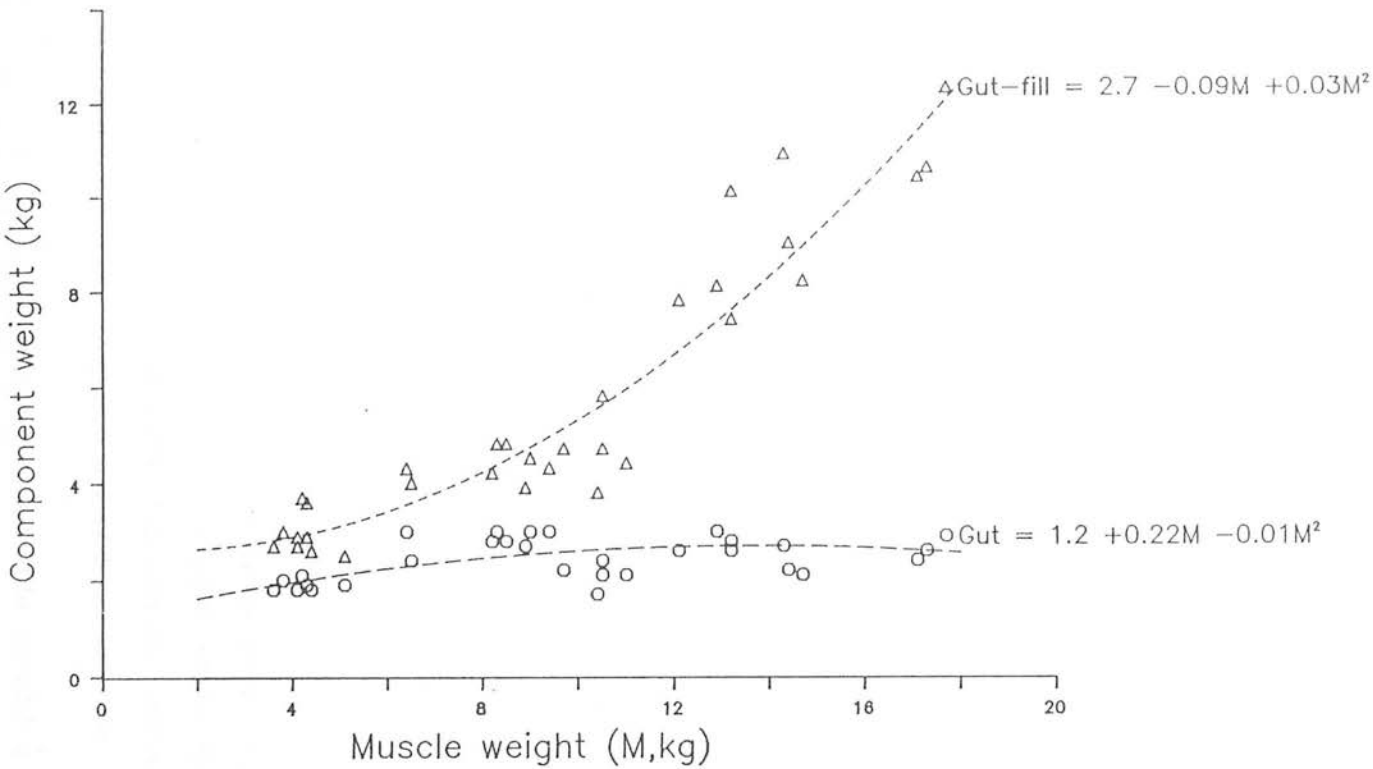


Fig. 1.2 The Relative Growth of Gut and Gut−fill in Scottish Blackface wethers (n=32) under non−limiting conditions

1.1.2.2 The Allometry of Chemical Components in the Body

Lawes and Gilbert (1859) analysed the empty-body (liveweight less gut-fill) of animals into four chemical components:

> The mineral matter [ash], the total dry nitrogenous compounds [hence protein], total fat [lipid], and water (the complementary quantity of the total dry matter).

later termed the 'Schematic Body' by Armsby (1908).

Since allometric analysis need not be confined to its original use of relating anatomical components (Huxley, 1932), log-log relationships may be fitted to chemical data to assess the suitability of the method in summarising mathematically the changes in composition of the Schematic Body.

Once again, the availability of data for sheep, published in an untransformed state, was limited. However, three sources of numbers were found. For relatively mature animals the data of Blaxter, Fowler and Gill (1982) and Lloyd *et al* (1985) were used and were supplemented with values for new-born lambs of 3kg given in ARC (1984). This procedure was justified on the basis that the regression analysis would not be sensitive to small errors in estimated composition at birth but a realistic reference point was required, outside the range of the actual data, in order to formulate sensible expectations for future tests. The other source of data was the study of Hodge (1974) for the growth of lambs given *ad libitum* access to milk from birth to 50 days of age. These data also served as a check of the first two analyses, since they were collected over a different range of maturity.

For all three data sets analysed here, protein weight was nominated the dependent variable and the natural logarithm of its value was plotted against the natural logarithm of the water, ash and lipid components. The allometric relations derived from regression analysis are given in Table 1.2.

The three sets of equations show little variability in the relationships of lipid, water and ash to protein, and a general agreement between breeds in their magnitude. The allometric method of analysis therefore appears to provide an accurate and simple summary of the change in composition of

Table 1.2 Allometric Growth Coefficients of the Chemical Components of Lambs given non-limiting conditions for growth

	Source and Breed	Maturity range	n	Water	(r.s.d.)	Ash	(r.s.d.)	Lipid	(r.s.d.)
1.	Blaxter *et al* (1982) (Suffolk X Finn Dorset wethers)	0.14-1.00	14	0.880	(0.054)	0.971	(0.196)	2.200	(0.226)
2.	Lloyd *et al* (1985) (Scottish Blackface wethers)	0.68-1.00	6	0.880	(0.060)	1.020	(0.141)	2.180	(0.280)
3.	Hodge (1974) [(Border Leicester X Merino) X Dorset Horn]	0.16-0.44	5	0.902	(0.007)	1.050	(0.045)	2.170	(0.058)

r.s.d. = residual standard deviation of the regression

lambs growing under ideal conditions. Moreover, the analysis shows that any of the four interrelated components could be used as a measure of potential growth. However, a component of the lipid-free empty body (protein) must still be favoured because the allometry of lipid varies under limiting conditions (see Chap. III).

The allometric description may be held to reflect the directives of the inherited growth-plan, that is, the composition that the lamb should take as it grows. The fattening characteristics of lambs growing under non-limiting conditions are termed 'desired fatness' or 'desired lipid : protein ratio' in Chap. II when the conditions necessary for the fulfillment of the potential are considered.

1.1.3 The Desired Rate of Growth

A simple method has been exploited for describing the change in form which the sheep undergoes during its attainment of maturity. The problem now remains to describe the maximum rate at which the form may be changed, a task which is reduced, by the allometric argument, to that of finding a mathematical prediction of the maximum (desired) rate of growth of muscle or protein weight.

The search for a universal growth function has been undertaken by biologists for over eighty years but, for the most part, prediction of the liveweight gain of mammals and birds has been their objective (Brody, 1945; Taylor, 1980c; Parks, 1982). Since liveweight has already been depicted as an unreliable measure of growth, unless taken across species of widely different mature size, their publications are employed here as a guide in methods of approach rather than for direct use.

The growth of the animal is taken to begin at conception and to be heading towards a stable, mature end-point. The applicable time relation of growth must therefore give an absolute growth rate which either abruptly becomes, or tends towards, zero. Preferably it will have an economy of parameters to which biological meaning may be attached and will exhibit properties of 'robustness and simplicity of parameter estimation' (Taylor, 1980b).

Such a list of specifications for the model discourages, at the outset,

adoption of the approach of Searle and Griffiths (1976,1983) whose theory of the growth of sheep takes the form of four disjunct 'phases', each of which requires its own set of parameters and estimated values. Of the more straight-forward models, simple linear or convex-shaped functions do not withstand even the common experience that the absolute growth-rate of a foetus never exceeds or equals that of a half-mature animal, thousands of times larger, growing at its potential rate. However, the growth curves of animals fed under non-limiting conditions do show a convex shape as they approach maturity, a phase which Brody (1945: p.484,Ch.16) regarded as the sequel to a geometric or accelerative phase of growth. He conducted his analysis by treating the two phases as separate, but they may just as easily, and effectively, be considered as parts of continuous or S-shaped curves, asserted by Laird, Tyler and Barton (1965) as the most promising functions to describe potential growth.

Laird *et al* (1965) subjected three well-known equations [the monomolecular equation of Brody (1945: p.543,Ch.16), the logistic equation of Robertson (1923) and the Gompertz (1825) equation, adopted for biological phenomena by Wright (1926) and Courtis (1937)] to an analysis against the liveweight data of several species. They dismissed Brody's curve on the basis that below the inflection point the actual data 'trail off to the left of the curve' primarily because Brody had treated growth rate as proportional to liveweight during the accelerative phase of growth. Functions of liveweight are better predictors of growth rate in that range and beyond, a criticism made by Parks (1982). Further analysis of the predicted specific growth rates of the logistic and Gompertz equations against actual data inclined Laird to a conclusion, voiced earlier by Courtis (1937), that

> the empirical finding that specific growth decreases exponentially with the age of the organism applies to the embryonic and post-natal growth of a variety of warm-blooded animals and hence their growth is satisfactority described by the Gompertzian growth equation. Laird *et al* (1965).

Furthermore, the Gompertz equation was found to be a useful predictor of pre-natal growth by Robinson and McDonald (1979) and ARC (1984) and was favoured by Emmans and Fisher (1986), who employed the function in the prediction of the rate of protein growth in the chicken. More recently, Emmans (1984,1985,1986,1987) extended its use to pig, cattle and sheep data. Whittemore and Tullis (1987) have also encouraged the use of Gompertz

analysis in the growth of pigs.

Consequently, the Gompertz equation in the form

$P_t = P_m \cdot \exp - [\exp (G_o - B.t)]$ (3)

where P_t = an immature protein (or muscle) weight at time t (days)

P_m = mature protein (or muscle) weight

B = the rate of attainment of maturity (d^{-1}); and

G_o = an initial condition = $-\ln [-\ln (P_t/P_m)]$

which has shown many of the properties required from a growth model (viz. accuracy, simplicity, and meaning) was elected the most suitable candidate for analysis of the rate of muscle gain of lambs fed under non-limiting conditions.

1.1.3.1 A Method for Estimating Parameter Values of the Gompertz Growth Equation

The value of the parameter B may be derived from the data by rearranging the equation such that

$$P_t/P_m = \exp - [\exp(G_o - B.t)] \quad (4)$$

$$\ln (P_t/P_m) = -\exp(G_o - B.t) \quad (5)$$

$$-\ln (P_t/P_m) = \exp(G_o - B.t) \quad (6)$$

$$\ln [-\ln (P_t/P_m)] = G_o - B.t \quad (7)$$

$$-\ln [-\ln (P_t/P_m)] = -G_o + B.t \quad (8)$$

then by letting $G_t = -\ln [-\ln (P_t/P_m)]$ (9)

$$G_t = -G_o + B.t \quad (10)$$

which is of the form $y = a + bx$ (11)

and disposes equation (10) to simple, linear reqression after an estimate of P_m has been made. (This task is more easily managed when the data set provides values of P_t close to maturity.) Any systematic upward or downward deviation from the estimated regression by the data when plotted as in equation (9) betrays either a false estimate of P_m (that is, it is too low or too high,

respectively) or inappropriateness of the Gompertz function. Should the regression survive the test of the data, the regression coefficient supplies an estimate of the value of the rate parameter B. The intercept gives a value for $-G_o$ and the standardised residual an estimate of the variability around the regression line.

1.1.3.2 The Potential Protein and Muscle Growth Rates of Scottish Blackface Lambs

The data of Lloyd *et al* (1985) have been analysed here in accordance with function (9) using a measured estimate for mature muscle weight, M_m, of 16.5kg. A low standard residual of 0.08, the absence of systematic deviation and the high r-squared value indicated a satisfactory correspondence between the form of the model and the data. The estimated B value was therefore 0.0081 (s.e. 0.0002) and G_o was -0.314, giving a description of the potential growth curve of muscle for these lambs as

$$M_t = M_m \exp - [\exp (-0.314 - 0.0081t)] \quad (12)$$

where M_m = 16.5kg

t = time in days from an initial muscle weight of 4.2kg.

Equation (12) is employed in subsequent experiments (Chaps. III and IV) to predict the expected potential muscle gain of Blackface wether lambs, and therefore serves as a standard by which to test the outcomes both of treatments expected to support the potential and those expected to fail.

The chemical data available in the literature for analysis of the protein growth curve of sheep under non-limiting conditions supply estimates of protein weight for either entire rams or foetuses. Emmans (1987) has suggested that an appropriate B^* (protein) value [4] for rams is 0.0224. This value is expected to be too high for wethers since they are known to grow at slower rates than entire animals (Hammond, 1932; Rhodes, 1969). The B^*(muscle) value of 0.0173 derived for muscle growth in SBF wethers may be more

[4] $B^*(\text{protein}) = BP_m^{0.27}$, that is, the B rate parameter is scaled to the mature protein weight of the breed (see section 1.3.1)

realistic. The suitability of this tentative estimate is assessed in the experiment reported in Chap. III.

1.2 A Theory to Describe Development during Potential Growth

Sections 1.1.2. and 1.1.3. proposed a resolution to the problem of predicting the rate and direction of the animal's impulse to grow into two simple, mathematical formulae. It is now the purpose of this section to depict the development of the whole post-natal lamb by means of combining equations (1) with (12) and then to structure a review of the abundant and well-established literature on growth and development around these deductions.

1.2.1 The Waves of Development

In his account 'On Growth and Form', Thompson (1917) pointed to direct relationship between the course of development in the animal and the rates of growth of the parts, since

> a very large part of the specific morphology of the organism depends upon the fact that there is not only an average, or aggregate, rate of growth common to the whole, but also a variation in different parts of the organism, leading towards a specific rate characteristic of each different part or organ.

Hammond (1932) adopted the same position concerning the development of the growing sheep when he stated, simply that 'the curve of liveweight growth is in reality made up of a number of curves of growth of different organs'.

From the two fundamental relationships already introduced, (1) that most of the chemical and anatomical components of the sheep increase allometrically to protein or muscle weight and (2) that potential growth of protein or muscle is traced by a Gompertz curve, it follows by mathematical argument that the increase in size of each component of the body during potential growth is given by its own Gompertz function sharing the same rate parameter value (B) as protein or muscle growth, that is, the same 'average, or aggregate, rate of growth common to the whole' required by Thompson.

For each organ or component (C), its own Gompertz function is derived from the value of its allometric coefficient (b values, Tables 1.1,1.2) in relation to protein or muscle weight, and the point of inflexion [t^* (protein)] of the protein muscle growth curve,

where $t^*(protein) = G_o/B$

and $t^*(component) = t^*(p) + [(\ln b) / B]$

such that the individual growth curve becomes

$$C_t = C_m.\exp - \{ \exp [-B (t - t^*(c))]\} \quad (13)$$

where C_t = immature component weight, kg

C_m = mature component weight, kg.

This method of analysis was employed by Emmans and Fisher (1986) for prediction of post-natal chicken growth and is used on the anatomical data of Lloyd *et al* (1985) with the derived values of b, $t^*(p)$ and B.The gain of some of the individual anatomical components are illustrated in Fig. 1.3.

1.2.2 The Order of Development

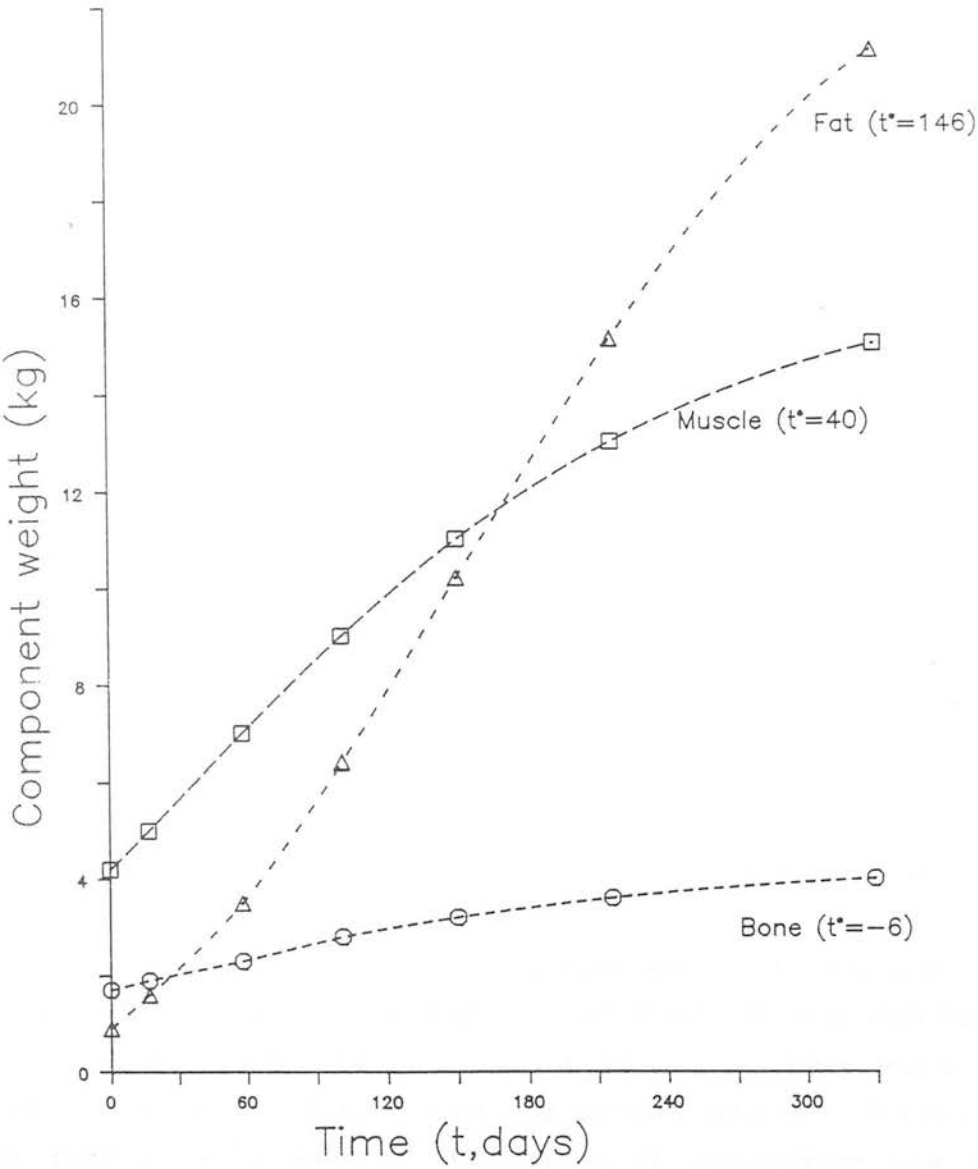
Hammond (1932) was also amongst those who contributed the opinion that

> the growth of different organs takes place in a definite order relative to the requirements of the animal.

which precipitated an investigation by the Cambridge workers into a functional interpretation of the order of development of farm animals. Palsson and Verges (1952) summarised the findings of this research in their statement that

> The major tissues of the body exhibit marked differential growth rates in post-natal life. The order of increasing growth rate with age follows an outward trend from the central nervous system, to bone, tendon, muscle, intermuscular fat and subcutaneous fat.

The Gompertz functions of the different components of the body lend themselves to analysis of the point of maximum growth, at $t = t^*(component)$ which occurs when $C_t = C_m/e$ at a rate $dC/dt = B(C_m/e)$. Consequently, the component Gompertz functions used to produce Fig. 1.3 served in addition as predictors of the sequence of development, outlined in Table 1.1, and they reveal the same trend as described by Palsson and Verges (1952). Furthermore, the order in which the fat depots matured (intermuscular fat before subcutaneous fat before kidney knob and channel fat before caul fat, Table 1.1) agreed largely with that recorded by McClelland and Russel (1972) for SBF



where t*= point of max. growth rate

Fig 1.3 The Derived Growth Curves of Body Components of Scottish Blackface wethers under non−limiting conditions

wethers and Russel, Doney and Gunn (1971) for SBF ewes. These workers found kidney knob and channel fat to be the last depot to mature and caul fat to be the penultimate.

The methods of anatomical dissection in this thesis do not reach to the level of detail as those of the Cambridge workers, since more attention is paid to the growth of the chemical body and the relation of growth to feeding. It is suggested, however, that a version of the proposed method of analysis could be employed for the relative rates of growth of, say parts of the musculature or skeleton. Using part-whole relationships, this line of research has been followed by Berg and Butterfield (1976).

The Cambridge workers, and others since then (Fowler, 1968) extended the functional view of development by relating the early maturity of the brain, eyes, lungs, kidney, heart, oesophagus, abdomen and small intestines to their 'vital functions to life' at birth, whilst those organs

> which have an unimportant function until after the lamb begins to consume fibrous foods (reticulo-rumen), or those whose function is largely that of storage of nutrients (fat depots)...develop mainly in the later stages of growth. Palsson and Verges (1952).

Such an attitude, however, had been criticised by Brody (1945: p.640,Ch.17) who, quoting Carrel (1931), asserted that the functional interpretation does not add to the understanding of the growth of animals since

> The significance of a given structural state is bound to the knowledge of the corresponding physiological state. Structure and function are two aspects of the same thing.

Gould and Lewontin (1979) took this point further, arguing that the flaw in the functional approach was the absence of an independent, empirical scale for the scientist to decide whether an organ was useful, or not, to the animal. The suggestion from these criticisms seems to be that biologists interested in growth make do with empirical descriptions of development free from functional interpretation.

1.2.3 The Growth of the Whole

1.2.3.1 Liveweight Gain

For completeness, the growth of the various components of the body can now be brought together to describe the gain in liveweight (LW) and the changes in the proportions of the LW as the lamb grows under non-limiting conditions. The interest shown by animal scientists in the LW growth curve is understandable when the advantages of picturing the progress of the whole animal and of taking direct and repeatable measurements of liveweight are appreciated. LW is also the most general way of describing sheep for the purposes of managing production systems. However, a problem persists in that there is no simple description of the LW growth curve because of the failure of gut-fill and gut components to adhere to an allometric relationship with any other component. However, by aggregation of the Gompertz curves of allometrically related components, the Gompertz equation can often give as good a description of liveweight gain as Brody's curves (Taylor, 1968; Tullis, 1982) or other more elaborate functions (for example, that of Moore, 1985).

Consequently, Gompertz functions have been fitted to the LW data of Lloyd *et al* (1985) and, with a measured estimate of the mature LW of 82kg, the B value for LW gain of SBF wethers was calculated to be 0.0076 (s.e 0.00014). Additional data, available from the same source, on the LW gain of Suffolk X Greyface wether lambs also provided a means of estimating the B value (0.0078, s.e. 0.00016) for a Gompertzian description of their LW gain. These two descriptions are used in following experiments as standards for judging the LW performance of test animals.

1.2.3.2 The Changing Proportions in the Body

The more immediate and measurable quantity of the animal's LW encouraged the custom of portraying the increase in weight of organs as a proportion of the LW, and then to outline the changes in these proportions with time. Hammond (1932) favoured such an approach but was also aware of the pitfalls of the analysis. A drop in the proportion of one component necessarily results in a rise in the proportion of the remainder. Consequently, changes in the form of the animal can become exaggerated particularly when used to interpret the effect of restricted feeding on growth and development (see Chap. III).

Lawes and Gilbert (1860) concluded from the analysis of proportions that the development of the sheep proceeds through

> a diminishing percentage of total offal parts and an increasing percentage of total carcase parts, as the animal matures and fattens, and of the internal parts, the loose fat alone [caul fat] increases both in actual weight, and percentage proportion, with the progress of the animals.

The findings of Hammond (1932) described a similar fall in the proportion of each of the offal components (head, pluck and liver), a near constant proportion of pelt, and a rise in the proportion of caul fat after birth. Moreover, he observed a fall in muscle and bone proportion, and an increase in fat proportion in the carcase as the lambs matured.

The availability of easily managed component growth functions derived from the data of Lloyd *et al* (1985) meant that the proportionate changes in the form of the LW of SBF wether lambs could be generated for a comparison with Hammond's findings. These derivations, presented for muscle, bone and fat in Fig. 1.4 show ample agreement with the trends described by Hammond (1932) and summarise the changes brought about in sheep growing at their potential rate. Similar changes were also mirrored in the calculated proportions of the chemical components in the Schematic Body. A fall in protein and ash, and a rise in lipid content of the empty-body during potential growth, was observed, in accordance with the now established views of chemical growth given by Armsby and Moulton (1925).

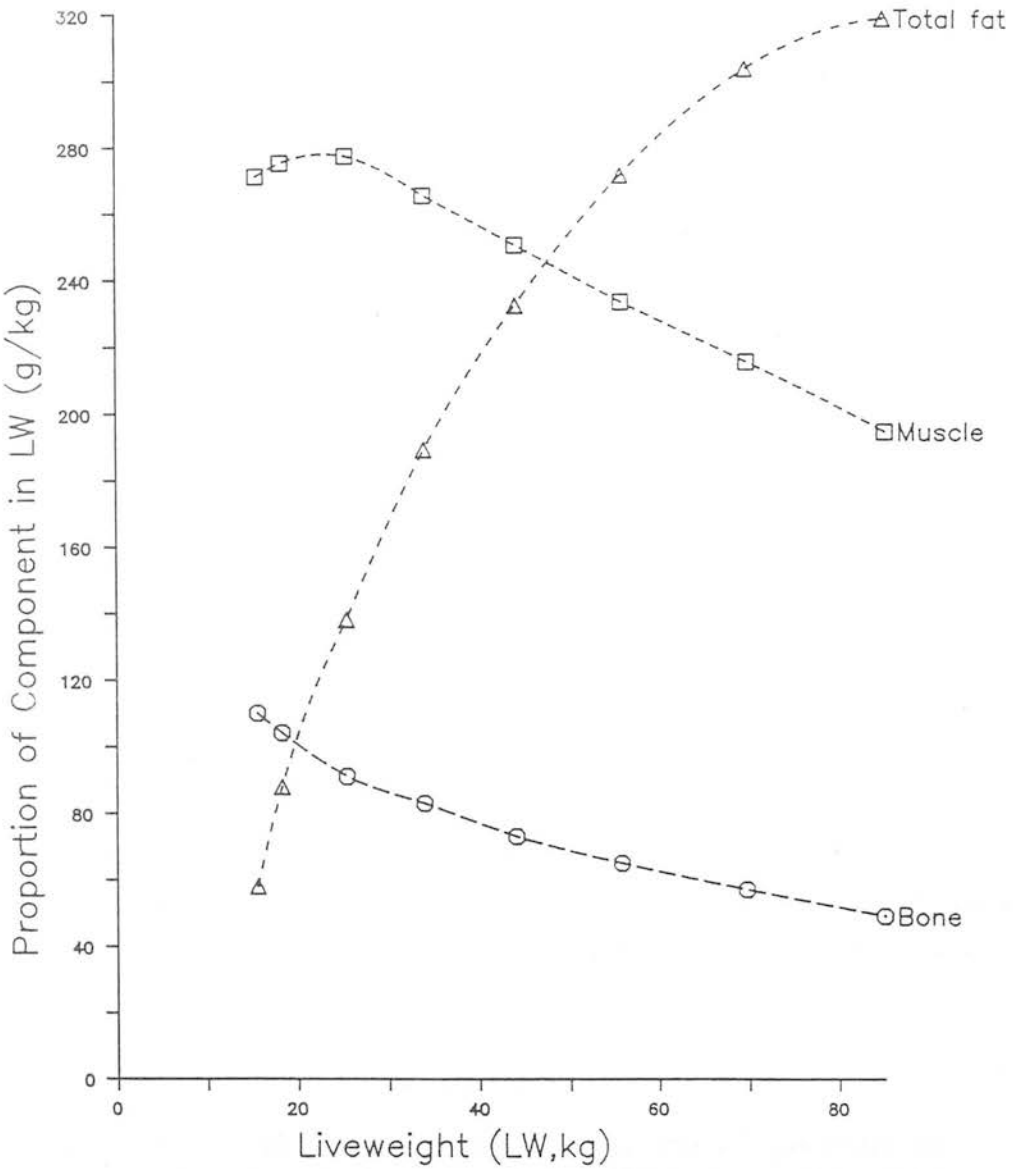


Fig. 1.4 The Derived Changes in the Body Proportions of Scottish Blackface wethers under non-limiting conditions

1.3 A General Statement on the Growth of Sheep

1.3.1 Standardising Potential Growth

The mathematical description of growth, outlined in the preceeding pages, is so far limited to predicting weight gains of the whole and parts of a sheep of a particular breed. It is not a general statement about the breeds which make up the species *Ovis aries* or about sheep as a species of mammal.

Thompson (1917), however, offered the hope to analytical biologists, who take a mathematical attitude towards the problem of growth, that

> we soon reach through mathematical analysis to mathematical synthesis: we discover homologies or identities which were not obvious before and which our descriptions obscured rather than revealed.

Brody (1945) took up this idea and pronounced that

> A fundamental characteristic of living things is that they are alike in general plan and different in detail.

His work, on a wide range of mammalian species showed the general nature of the interspecific relationship between mature size and time taken to mature (i.e. the larger the animal, the longer the time), but his work was left largely undeveloped. Gunther and Guerra (1955) joined in the expansion of these ideas with a theory of biological similarities based on dimensional analysis. However, Taylor (1965, 1968, 1980a,b,c) offers the most complete proposals of 'genetic size-scaling rules' for standardising mammalian growth curves, with respect to the genetic differences in body size.

The rules, reported in his 1980a paper are:

> 1) Treat all age and time variables for the i^{th} genotype as directly proportional to $A_i^{0.27}$ where A_i is the mature body weight of the i^{th} genotype.
>
> 2) At every age standardised treat all cumulated inputs and outputs for the i^{th} genotype as directly proportional to A_i

The value of the exponent in rule (1), 0.27 or 1 - 0.73, has been empirically derived from large and diverse sets of data on the mature body weights of mammalian species, handled firstly by Brody and latterly by Taylor.

1.3.2 A Comparison of Breeds

The method of Taylor (1980a) can be used to formulate the general proposition that there are no differences in the potential growth of different sheep breeds once their growth curves have been standardised by application of the scaling rules. It is suggested that standardisation of the growth curves of, in this instance, different sheep breeds, and a comparison of the curves with an empirically derived mean for all sheep would indicate deviations that could not be expected once the differences in mature size had been accounted for.

Unfortunately, few experimenters have tested sheep breeds by comparing their standardised potential growth curves across wide ranges of maturity. Seldom are the data reported in a form on which an independent analysis can be made and frequently it is evident that the lambs were reared under restricted or constrained feeding regimes. In these cases the experiments are a test of a genotype's response to limiting environmental conditions rather than a definitive description of the breed.

Lawes and Gilbert (1859), Hammond (1921) and Palsson (1950) compared the body composition of a large number of breeds and crosses, under various feeding regimes, thereby describing each as 'early-maturing' or 'late maturing'. Theoretical and experimental investigations since then conclude that these descriptions broadly, and simply, correspond to 'small' and 'large' mature size.

McClelland, Bonaiti and Taylor (1976) made a standardised comparison of breeds, and chose the Soay, Southdown, Finnish Landrace and Oxford Down breeds to test the body composition of sheep across a wide range of mature sizes. Their experiment ran from 0.4 to 0.7 maturity. Breed and sex differences were reported to have 'disappeared' at the same degree of maturity when the data were expressed as percentage proportion of body or carcase weight. Only the Soay breed showed significantly less fat in its body than the other breeds, a finding which Hammond (1932) attributed to the immaturity of the semi-wild Soay when compared with domesticated and improved breeds. The Soay may have to be regarded as an exception to the rule.

Searle and Graham (1972), Kempster and Cuthbertson (1977) and Theriez, Tissier and Robelin (1981) also report that breed differences at the same

degree of maturity, if found, are usually small, and mostly associated with fat deposition. Since the fat depots are such a variable component of the empty body, caution must be exercised in drawing conclusions from such breed 'differences' which could arise if some of the animals were not given non-limiting conditions for growth (see Chap.II). Butterfield *et al* (1983) reported no differences in the growth and development of large and small strains of Australian Merinos after scaling for mature size.

McClelland and Russell (1972) offered evidence to show that fat distribution varies between breeds, for instance, down breeds showing more subcutaneous fat than mountain breeds which have larger internal fat depots. Despite the differences in distribution, however, the authors suggest that the total proportion of fat in the body at the same degree of maturity may remain the same. Lawes and Gilbert (1859) drew attention to these type differences in their early comparisons of sheep breeds.

The nutritional histories of the cross-bred lambs of Fourie, Kirton, and Jury (1970), Vesley and Peters (1972), Carter and Kirton (1975) Oskowski and Borys (1976), More, O'Ferrall and Timon (1977) and Wood, Macfie, Pomeroy and Twinn (1980) are, at best, described only vaguely, which limits the scope for conclusion from these studies. Only Wood *et al* (1980) make an attempt to relate their findings to degree of maturity.

However, More O'Ferrall *et al* (1977), Wolf, Smith and Sales (1980) and Notter, Ferrell and Field (1984) unite in concluding that Dorset Down crosses have a higher fat content than other breeds. They are, nevertheless, a small breed (c. 77kg, Croston and Pollott, 1985) and would therefore be expected to have a higher proportion of fat in their bodies when killed at similar LWs to the larger breeds.

The data of Wolf *et al* (1980) and Latif and Owen (1980), and the analysis of Cameron and Drury (1985), showed Texel crosses to have a higher proportion of muscle in their bodies than crosses from other sire breeds. Only Cameron and Drury (1985) make a standardised comparison to strengthen their conclusions.

It would seem necessary, however, before drawing conclusions, to subject sheep breeds to a considered and systematic comparison, employing standardising techniques for analysing the growth data of lambs reared under

non-limiting conditions. The comparison of breeds under conditions where insufficient attention has been paid to the nutrition of the lambs come under particular criticism since it will be demonstrated in Chaps. II and III that the fattening characteristics of sheep are highly sensitive to feeding.

CHAPTER 2
NON-LIMITING CONDITIONS FOR THE GROWTH OF SHEEP

2.1 Introduction

In Chapter I the idea was introduced that an animal inherits a growth-plan, coded in its genotype, which determines, for that individual, the upper limit to the path of its growth towards full fecundity at a certain mature end-point. The potential growth of the organism is then manifested and becomes actual, when the material increase in mass accords with that of the intended growth-plan. However, Aristotle's further observations on animals suggested that what distinguishes their existence from that of a plant or a non-living rock, is that an animal

> is that which moves itself, that the origin of this is unmoved, and that the first mover must necessarily be unmoved De Motu Animalium.

Aristotle seems to have been asserting that the animal inherits, from the moment of conception, not only a coded growth-plan in its genotype, but also a motivation and a means by which to attain the potential of that plan. Orexis (appetite) was a result of the motivation to fulfill the growth-plan. That the genotype of 'successful' parents provides their offspring with all they need to be able to fulfill themselves is still fundamental to theories of organic evolution.

2.2 The Material Resources of Growth

To Empedocles (c. 493-433 B.C.) and, after him, Aristotle, matter took one of four forms--air, water, fire and earth--which today's biological chemist would interpret, respectively, as oxygen, water, energy, (yielded from the food) and the building blocks of the body, also found in the food, namely proteins and minerals. The appetite of an animal is thus for these four material resources. However, in the context of feeding behaviour, the term appetite is used strictly in the sense of desired feed intake (DFI), that is, the quantity of feed required

to provide what is necessary to satisfy the demands of the growth-plan.[5]

In animal science it is taken for granted, in all experiments except those with aquatic species, that the individual may be left to decide how much air, and of what quality, it needs. Commonly, an animal is also trusted to regulate its own intake of water, in relation to its intake of other resources. It is thought important to bear these facts in mind when considering the viability of the extension (to the view that an animal can choose what air and water it needs) to that which recognises the animal's desire for the 'fire' and 'earth' found in its food. Since Forbes (1987) has reviewed the evidence which supports the belief that animals are capable of adjusting their intake of energy ('fire') according to their needs, the more coherent view should hold that the animal also possesses the ability to choose, from each of the four elements including the 'earth', a combination of resources which provides what it needs to satisfy its growth-plan. Some choices may be more difficult to make, or less pressing than others. Choices about air or water intake may then be seen as urgent requirements because of the time-scale on which the effects of deprivation of these resources are measured. Choices about the rates of food resource intake, however, may be rapidly changing, of marginal benefit to the animal, or more complex in nature. They may therefore be less readily apparent to observation. This view depends largely on the type of description made of the 'fire' and 'earth' in the food.

Armsby (1908) affirmed his 'Principles of Nutrition' on the century-old basis that both the food and the animal can be related to one another in terms of matter (earth) and energy (fire). Together they form a system in chemistry which complies with the laws of thermodynamics laid down by Mayer and Helmholtz (Kleiber, 1961). A full chemical description of the set of material resources found in food consists of a lengthy list of organic and inorganic molecules, which includes the categories carbohydrate, lipid, amino acids, minerals and vitamins. Here, for the time being, the dry matter of the food (henceforth called feed) will be regarded simply as yielding three components, namely ash, protein and energy. The 'earth' building-blocks are in the form of either non-organic matter (ash) or nitrogenous organic matter (protein). That

[5] There is, therefore, no place for the usage of the term appetite as 'the amount of feed which the animal eats' since only one case satisfies this condition, i.e. when DFI = actual feed intake. The important distinctions between actual and desired feed intake are addressed subsequently.

portion of the digested protein which is not stored is catabolised, and yields energy. Part of this energy yield may be used by the animal for its own purposes, i.e. the metabolisable energy yield of protein. This quantity must be added to the energy yielded by the non-nitrogenous organic matter to give the total energy (metabolisable energy) fraction of the feed. The remainder is lost from the animal in the urine.

The fulfilled growth-plan of the sheep, as best it be known, has already been described in chemical language as a certain desired rate of gain of protein matter, associated with strict but changing ratios of protein to water, to ash and to lipid. This stored, or retained, matter can conveniently be expressed at the same time as a store of potential energy. Therefore, the correspondence between animal and feed in chemical descriptions permitted the first nutritionists (reviewed by Armsby, 1908) to assert that an animal has a set of resource requirements [6] from its feed, which Waters (1908) summarised as having the following uses to the animal:

> We have assumed that the uses to which an ungrown animal puts its feed are divided as follows:
>
> (a) Maintenance
>
> (b) Production of Growth [protein + water + ash]
>
> (c) Production of Fat [lipid]
>
> That the full and complete requirements of maintenance must be satisfied before any sort of production can occur, and that after the maintenance requirement is fully satisfied, the production incident to the offering of feed in excess of maintenance will take the form of growth, up to the limit in rate of the capacity of the animal as determined by heredity. Any food supplied above these two requirements, and up to the limit of appetite, and the digestive and assimilative capacity of the individual would be stored in the body as fat.

In this scheme, gain of protein, water and ash are distinguished from fattening, and the former are seen as having priority for the resources during the growth period.

In this thesis, reference is made to the metabolisable energy (ME)

[6] that is, a rate at which the animal needs to be supplied with energy or a nutrient in order to survive, grow and fatten (Emmans and Fisher, 1986).

requirements of the animal (the basis of the ARC, 1984 system) for the illustration of key ideas in nutrition and the formulation of feeds and the testing of outcomes in the experiments. Where a second test has been necessary, the prediction equations of Emmans (1988) for effective energy requirements have been employed. The problems of finding a suitable scale on which to measure the protein yield of feeds and the requirements of ruminants are presented later in relation to the concept of nutrient: energy (that is, ME) ratio of the feed.

2.3 A Theory of the Conditions which are Non-limiting to Growth

The old idea that an animal seeks what it needs, from its environment, to survive and to express its potential for growth and fattening requires the definition of those conditions under which non-limited fulfillment of the growth-plan may be expected, that is, the conditions under which the appetite, or desired feed intake (DFI) is satisfied.

Assuming a ready availability of air and water, four necessary conditions may be distinguished:

(i) the feed must be freely given *ad libitum*.

(ii) the feed must not constrain intake to a level below DFI through its bulkiness.

(iii) the feed must not limit intake to a level below DFI through its toxicity.

(iv) the feed must not be first limiting in a nutrient. When the total feed intake yields the desired energy intake, the ratio of protein to energy and ash to energy in the feed must give at least the desired quantity of those nutrients.

2.3.1 The Necessity of Free Feed Supply

That the first necessary condition is free and continuous *ad libitum* access to at least one feed obviously precludes the feeding of restricted quantities of any feed if the animal is to express its potential for growth. The response of the animal to the imposition of limiting nutritional conditions are the subject of Chapter III.

2.3.2 The Influence of Feed Bulkiness

However, *ad libitum* access to the feed supply is a necessary but not sufficient description of non-limiting conditions, since only a subset of all feeds, fed singly *ad libitum*, can satisfy the needs of the animal.

For instance, a growing lamb, given *ad libitum* access to a single feed, will require a certain quantity to satisfy its appetite for energy and protein, but if the feed were progressively diluted by an inert filler (e.g. sand or lignin) the 'bulkiness' of the feed may prevent the animal from eating the feed at an adequate rate. Feeds which are well-known to be limiting in this way are roughage feeds such as hay, silage and straw (Blaxter, 1962; Balch and Campling, 1962 and Campling, 1964) and the growing lamb is often subjected to feed constraint by bulk (Campling, 1964). However, scales for measuring bulkiness in feeds have not been found reliable across all feeding conditions. Van Soest (1965) suggested a relationship between cell wall constituents and feed intake of roughages. Baile and Pfander (1967) claimed greater accuracy through the measurement of the bulk density of the feed. Davies (1962) showed that decreasing dry matter content of feeds could also be regarded as increasing their bulkiness. Waldo (1986) reviewed old and current ideas on the capacity of ruminants for bulky feeds and discussed the recently proposed INRA fill unit system which describes feeds by their 'fill value' relative to a standard or reference forage.

Bulky feeds therefore contain a large proportion of undegradable matter, either in the form of inert ash, water or indigestible organic matter such as plant cell walls and lignin. Commonly, such feeds are associated with low protein contents (Henry, 1902). Bulky feeds also result when their constituents have a large particle size. For example, unchopped straw is bulkier than ground straw because the former requires more chewing and regurgitation, and, therefore, the rate of intake is slower (Balch and Campling, 1962). If the animal cannot recover this deficit by eating for longer in the day, it will have a constrained feed intake (CFI) which will fail to satisfy its appetite for one or more resources (CFI less than DFI).

The capacity of a ruminant for bulk is not only a reflection of the physical

volume of its reticulo-rumen, which develops most when stimulated by the intake of roughage feeds (Wardrop, 1960), but also the ruminant's capability to chew and digest coarse fodders (Campling, 1964). The low protein content of most roughage feeds renders them less digestible (more bulky) because the microflora rely on a certain nitrogen supply to support their own growth, and hence their fermentative activity (Johnson, Hamilton, Mitchell and Robertson, 1942). Egan and Moir (1964) showed that infusions of urea increased the digestibility (and thus, intake) of a low protein basal feed given to sheep.

The theory of a desired feed intake (DFI) asserts that an animal will try to eat enough of a given feed to satisfy its appetite for the first resource (nutrient or energy) limiting to growth. Therefore, taking animals with the same capacity for bulk and capacity for growth given feeds of uniform particle size, the theory predicts that actual feed intake will initially increase as the proportion of undegradable matter (bulk) in the feed increases. Conrad, Pratt and Hibbs (1964) showed, in the cow, that this was the case as feed digestibility fell from 0.8. Owen, Davies and Ridgman (1969) and Dinius and Baumgardt (1970) report analogous examples in sheep. At a critical bulkiness (digestibility), actual feed intake will be maximised, when bulk intake reaches the bulk capacity of the animal. In the experiment of Conrad *et al* (1964) this point was found to be at an equivalent digestibility of 0.67. From this point, as digestibility falls further, actual feed intake will decline as the animal's intake becomes increasingly constrained by its capacity for bulk.

2.3.3 The Interference of Feed Toxicity

The effect of toxins in feeds on the health and feed intake of animals is a broad and complex topic. At one extreme, poisons such as strychnine and cyanide, are immediate and lethal in their action, whilst toxic metals, such as lead and cadmium, can be immobilised in the bones, teeth and brain, and despite high levels of intake over many years may never show any destructive effect on the animal. However, should the animal become stressed, or fevered, the accumulated metal is released into the bloodstream, causing widespread metabolic disorder (Duffus, 1980). For the most part, toxins in feeds result in a fall, or temporary cessation, in feed intake whilst the animal degrades, immobilises or excretes,up to a certain threshold,the offending substance (Duffus, 1980; Clarke, Harvey and Humphreys, 1981).

2.3.4 The Desirability of Ideal Feed Balance

When describing freely-offered, highly digestible, non-bulky, non-toxic feeds in terms of their nutrient: energy (ME) ratios, they are found to divide conveniently into two sets, with respect to the needs of the animal. The first set are those which are first limiting to growth in a nutrient. These feeds are imbalanced and often limiting to growth since the animal must exceed DFI (energy) in order to acquire its DFI (nutrient). In this case DFI (nutrient) may not necessarily be achieved before intake is constrained by heat stress or feed capacity. The other set of feeds is not first limiting to growth in a nutrient. These feeds are not limiting to growth but are imbalanced in relation to the animal's needs because the animal must process an excess nutrient intake whilst attaining DFI (energy).

It follows that for a given nutrient there is only one nutrient: energy ratio, which is both balanced and non-limiting to growth because it allows the animal to satisfy the unique and ideal condition of DFI (nutrient) = DFI (energy) when in a given state and environment. Considerations of the balance of protein and energy in the feeds given to a ruminant must first be treated conceptually, since it is not easily possible to make a reliable numerical analysis of the ideas that survives testing against the plentiful data on the subject. Scales for measuring the actual supply of protein to the animal (truly absorbed amino acid nitrogen, TAAN, Oldham and Webster, 1986) are still being developed (INRA, 1978; ARC, 1984; Madsen, 1985; NRC, 1985). There is universal recognition that in the ruminant the protein yield of the feed is partly dependent on the metabolisable energy yield which means that energy and protein, as a balance in the feed, cannot be treated as independent.

The concepts employed in most of the quoted systems for predicting the protein supply of feeds are typified by the proposals of ARC (1984), Chapter IV. The microflora of the rumen are known to synthesise protein during their own growth (protein which is eventually yielded to the animal) from both non-protein (NPN) and protein-nitrogen in the feed. The product of microbial synthesis (microbial amino acid nitrogen, ARC 1984) is dependent on the supply of degradable nitrogen (RDN) and the energy-yielding component of the feed. The remaining component of the protein in the feed is undegradable (UDN), part of which is digested and absorbed by the animal, adding to TAAN, and part

of which is voided in the faeces (FN).

Nevertheless, it is conceivable that a subset of all single feeds will be non-limiting to growth i.e. when DFI (energy) is greater than or equal to DFI (nutrient). Single feeds, rich in protein and ash (high nutrient: energy ratio) will permit the animal to express its potential for growth, provided that the animal can process the excess nutrients consumed, as it attempts to satisfy its DFI (energy). Single feeds with low nutrient: energy ratios, however, will be limiting in some cases, since the animal will satisfy its requirements for energy before gaining sufficient nutrients to attain its potential rate of growth. A simple numerical example can be taken to illustrate this point, using typical values for a 20kg Blackface lamb.

Suppose that the lamb is seeking to grow protein at a rate of 30g/day, and gain lipid at 90g/day (Chap. I) and that a feed A containing 0.14 DCP and yielding 10 MJME/kg is perfectly balanced [i.e. DFI (protein) = DFI (energy)] for the lamb at a rate of intake of 0.9kg/day. From the knowledge that:

MEI = ER + H

where

MEI = metabolisable energy intake,

ER = energy retention and

H = heat loss

and that the potential energy of stored protein is 23.8kJ/g, and of lipid is 39.6 kJ/g, the heat loss in this case must be 4722kJ/day [See Table 2.1, case (a)].

If a feed B, with the same yield of ME but a protein content of 0.10DCP, is now given to the lamb (and, for simplicity, all DCP is assumed to be of equal quality), the intake of feed is expected to rise to 0.9 X 0.14/0.10 = 1.26kg, as the lamb attempts to satisfy its DFI (protein) of 126g/day. The surplus consumption of energy (3600kJ) may be dissipated as heat or stored as lipid [case (b) Table 2.1]. If the lamb is assumed to use ME for lipid synthesis with an efficiency of 0.50, the lamb can convert the 3600kJ above its DFI (energy) into 45g of lipid (1800 kJ/39.6) and must consequently lose 1800kJ more heat.

Table 2.1 A Theoretical Illustration of the Concept of Protein: Energy Balance of Single Feeds offered *ad libitum*

		(a) Feed A (0.14 DCP, 10 MJME/kg)	(b) Feed B (0.10 DCP, 10 MJME/kg)	(c) Feed B	(d) Feed B
(i)	Desired feed intake (g/day)				
	for protein	900	1260	1260	1260
	for energy	900	900	900	1260
	for first limiting resource	900	1260	1260	1260
(ii)	Total feed intake (g/day)	900	1260	900	1260
(iii)	Energy balance (MEkJ/day)				
	intake	9000	12600	9000	12600
	stored as protein	714	714	510	714
	stored as lipid	3564	3564	3768	3564
	heat	4722	6522	4722	8322
	surplus (as lipid)	0	1800	0	0
(iv)	Rates of gain (g/day)				
	protein	30	30	21	30
	lipid	90	135	95	90
(v)	Feed Description	Balanced Non-limiting	Imbalanced Non-limiting	Imbalanced Limiting	Balanced Limiting

If the lamb is able to dissipate the extra heat generated, it will still attain its potential growth, by the definition given as a progressive increase in protein weight towards maturity, and the feed may be considered non-limiting to growth. However, the lamb has been obliged to exceed its desired lipid:protein ratio at a given degree of maturity, as an adaptive response to a sub-optimal feed and is therefore not adhering to the directives of the growth-plan, its 'true' potential. Feed B, in case (b), is therefore an imbalanced feed which is not limiting to growth.

As the protein content (g/kg) of the single feed offered falls further, feed intake is predicted to increase in relation to the protein requirement (g/day) until the lamb can no longer synthesise and store the necessary extra lipid and dissipate the surplus heat, or accommodate the larger volume of feed consumed, whichever constrains intake first. At this point, the lamb fails to meet its DFI (protein) and the feed, though offered *ad libitum*, is limiting to growth.

For the examples in Table 2.1, where the lamb is growing protein fast in relation to its rate of lipid gain, it is expected that the feed conversion ratio (g feed intake per g gain) will rise on lower protein content feeds because lipid will contribute a greater proportion to the empty body gain. Also, if the lamb is able to dissipate the extra heat, the empty body gain on the low protein content feed will exceed that on the higher protein content feed because of the surplus lipid gain. An increase in the *ad libitum* feed intake and an increase in the feed conversion ratio following the introduction of a single feed of low protein content has been shown in sheep (Ranhotra and Jordan, 1966), chickens (Kirchgessner, Roth-Maier and Gerum, 1978) and pigs (Kyriazakis, Emmans and Whittemore, 1987). Their data are presented in Table 2.2.

However, the necessity for a homeothermic animal to lose the excess heat generated in using a certain intake of feed for tissue synthesis means that the idea of a balance between nutrient and energy in the feed must be considered in relation to the environmental temperature, since the desire of the animal to remain thermally neutral with respect to its environment governs the actual balance of a given feed intake at a given ambient temperature. Thermoneutrality is achieved when DFI (nutrient) = DFI (energy) and the animal is in balance with the warmth of its environment in such a way that it need not increase its heat loss nor generate extra heat in its body to maintain its

Table 2.2 The Measured Feed Intake and Growth of Sheep, Chickens and Pigs given *ad libitum* access to Single Feeds of different Crude Protein Content

Species	Feed Identity	Crude protein content of the feed (g/kg freshweight)	Total feed intake (g/day)	Liveweight gain (g/day)	Feed conversion ratio (g feed/g gain)
Sheep[a]	1	110	1239	300	4.14
	2	140	1280	320	3.95
	3	165	1170	300	3.91
Chickens[b]	1	160	146	66	2.22
	2	210	136	68	1.98
	3	260	133	68	1.96
Pigs[c]	1	131	1090	530	2.05
	2	225	900	690	1.30
	3	332	860	660	1.28

Data sources: [a] Ranhotra and Jordan (1966)
[b] Kirchgessner, Roth-Maier and Gerum (1978)
[c] Kyriazakis, Emmans and Whittemore (1987)

desired internal temperature.

The idea of thermoneutrality, and its relation to the balance of the feed, is best illustrated by referring to the theoretical case considered in Table 2.1. In that instance, the assumption that the excess energy intake could be disposed of by laying down lipid and losing extra heat, meant that the lamb is case (b), on the imbalanced feed, could increase its intake of energy in order to reach DFI (protein). However, if it is supposed that lamb (b), Table 2.1 on the 0.10 protein feed, is not able to dissipate the extra 1800kJ of heat which it must to reach DFI (protein), then ME intake will be constrained to 9000kJ (0.9kg of feed) and DFI (protein) will not be attained [case (c), Table 2.1]. Putting aside the problem of maintenance protein requirement and taking the same value for the efficiency of protein use, 0.238 or 30/126 as in case (b), Table 2.1, it may be deduced that the lamb will store only 510kJ as protein, the remainder of its ME intake being directed into lipid retention (3768kJ), allowing dissipation of the imposed 4722kJ of heat. In this way the animal remains thermally neutral at that temperature but the feed is both imbalanced and limiting to growth.

Only when the lamb is put into a colder environment, on the low protein content feed, will it be able to lose the necessary extra 3600kJ through the increased energy cost of maintaining its internal body temperature. In consuming 1.26kg of feed, it will reach DFI (protein) and grow at its potential rate [case (d), Table 2.1). The 0.10 protein content feed will then be balanced and non-limiting for that lamb at that ambient temperature.

An experiment made by Andik, Donhoffer, Farkas and Schmidt (1963) showed how strongly environmental temperature can influence the effective balance of nutrient and energy in a feed by altering DFI (energy) relative to DFI (protein). At room temperature (20-25°C), rats offered a feed *ad libitum* with 0.04 crude protein, ceased to grow, and died, because they failed to obtain enough nutrient before heat stress constrained their intake. When the same feed was offered to the rats at 5°C ambient temperature, they doubled their feed intake, achieved a higher nutrient intake and grew well because the cooler environment increased their energy requirement for the achievement of thermoneutrality. Gibb and Penning (1972) showed a similar but less dramatic effect on feed intake and growth of milk-fed lambs at three different environmental temperatures.

Finally, returning to the main argument, the ideal balance of nutrient to energy in a feed may also be expected to change as the animal grows. In Chap. I, it was shown that protein growth-rate reaches a maximum at a degree of maturity, u = 0.367 or Pm/e, where Pm is the mature protein weight and e is the base of natural logarithms. Lipid contributed an increasing proportion to the gain of the empty-body as the lamb matures. If maintenance energy requirement also increases at the same rate with maturity as maintenance protein requirement (Emmans1988), it may be predicted that an ideally balanced feed for a new-born lamb (in which lipid makes a small contribution to the empty-body gain) has a higher nutrient:energy ratio than that required by the same lamb when it has passed the point of maximum protein growth. The ideal balance would therefore be expected to fall systematically as the lamb matures.

Therefore, in this review of the nutrition of animals, the definition of non-limiting conditions for the expression of potential for growth has emerged as *ad libitum* access to a balanced feed which does not constrain intake by its bulkiness, and which is free from toxins.

2.4 The Provision of Non-limiting Conditions for Growth

Pursuing the theme that:

(i) animals inherit a growth-plan,

(ii) animals have a need for certain resources to meet the specifications of the growth-plan,

(iii) animals inherit a motivating desire, called appetite, to acquire each of these four resources,

it follows that there are only two ways of providing non-limiting conditions for the growth of animals, namely:

a) *ad libitum* access to a single feed which is not first limiting in a nutrient

b) *ad libitum* access to a set of feeds, a possible *combination* of which is not first limiting in a nutrient.

2.4.1 Non-limited Growth on a Single Feed

The entire argument of Chap. II so far was used to justify the adoption of the data of Lloyd *et al* (1985) in an analysis of the potential for growth in sheep in Chap. I. The lambs in that experiment, offered *ad libitum* access to a single feed which contained 158g CP/kgDM (source: soyabean and fishmeal) and a vitamin/mineral supplement, conformed in their feed intake characteristics to the pattern expected by a theory which predicts the energy requirements for maintenance, growth and fattening (Emmans, 1987).

Further data are presented in Exps. 2, 4 and 5 to verify that *ad libitum* feeding of single feeds with high nutrient: energy ratios is a suitable method for permitting an animal to express its potential rate of growth and change in form.[7] Indeed, *ad libitum* access to single feeds is one of the most established methods of feeding growing animals 'to appetite' (McMeekan, 1940; Searle *et al*,

[7] And, conversely, or rather interdependently, that the methods of describing potential growth in Chap. I retain their usefulness upon further testing.

1972; Parks, 1982; Thompson and Parks, 1982). However, it is important to remember that the animal under this feeding regime is not given complete freedom in which to discriminate between its appetite for energy and for a certain nutrient in its diet. It can never have the chance to choose an ideal and changing feed balance and could become constrained if its required feed balance rose above that supplied in the feed, during the occasion of increased environmental hotness.

Consequently, it would lead to greater surety on the part of the experimenter of the provision of non-limiting conditions for growth if the animal were introduced watchfully to a range of feeds of widely different nutrient: energy ratios and left to make a free choice of its own diet.

2.4.2 Non-limited Growth on a Set of Feeds

Therefore, an alternative way of providing non-limiting conditions for the growth of animals is to give each individual a free choice of the type and quantity of each of the four resources it requires.

Stabler (1911) and Evvard (1915) adopted this approach when they offered growing pigs a continuous, *ad libitum* choice between any of seven feeds (whole corn grain, meat meal, whole oats, charcoal, oil meal, limestone and salt). They expected that, from the diverse choice of feeds offered, the pigs would find a non-limiting combination (a diet) because they considered 'the appetite of swine a reliable indicator of physiological needs'.

On the basis of his results, Evvard (1915) commended the free-choice system of feeding since it,

> enabled and encourages maximum development: in other words actually permits the inherited specifications to be fulfilled to all intents and purposes.

Evvard's pigs had grown well; some had gained weight faster than any previously recorded at the Iowa Agricultural Station. He also stressed the finding that, as the pigs grew, they maintained a varying balance between protein and energy in their total feed intake by changing the proportion of each of the feeds in the selected diet. When young, the pigs chose a diet rich in protein, then, as they became larger, they ate a smaller proportion of the protein-rich feeds in their diet.

Ad libitum access to more than one feed, a possible combination of which is not first limiting in a nutrient, would appear to have been a viable alternative, if not an improvement, on its lesser cousin, *ad libitum* access to a single feed. Indeed, since Evvard's enthusiastic debut, there has been much experimentation carried out on the topic of choice-feeding (though not always with a strictly nutritional objective) in which many species have been subjected to a range of options. The data from these experiments may be used to challenge Evvard's view about the animal's ability to discriminate between feeds by asserting a set of 'Rules of Diet Selection' that the animal should follow if it is to optimise its diet. If the expectation that an animal exercises its choice in directed manner is fulfilled, it will then be possible to decide upon the suitability of choice-feeding as a reliable technique in future assessments of the animal's nutritional requirements.

2.5 Rules of Diet Selection

The animal is assumed to have an appetite, or desire, to fulfill its growth-plan, and also to have a faculty of discrimination . It may be deduced, therefore, that the animal will search amongst all the feeds on offer until it succeeds in acquiring a non-limiting, or optimal, diet for growth. Following domestication, any relaxation of the fundamental ability of the animal to select for itself an adequate diet, and hence to survive and remain fit in the population, is considered to be minor in relation to the vigorous selection pressure which had operated on the wild ancestor for thousands of years. The trait of 'nutritional wisdom' is expected to have an underlying importance to the individual and to be strongly exercised in domesticated species, particularly in extensive systems of husbandry.

Models to predict the normative, or desired, behaviour of animals when foraging (i.e. the behaviour which the animal ought to do to obtain the most advantageous option according to some functional criterion, Krebs and McCleery, 1984) will incorporate considerations of both the nutritional objectives of the animal (induced by the direction of growth towards maturity and reproductive capability) and the conflicting demands on the animal of, for instance, predator evasion and the overcoming of obstacles to feed recognition. Theories of the learning behaviour of animals help prediction of short-term decisions made when the animal is offered a new, unfamiliar feed, or longer-term decisions when the animal continues to seek information about its environment (Krebs and McCleery, 1984).

The proposed rules of diet selection form a theory which attempts to predict the outcome of all the possible types of experiment in which an animal, in its desired state at a given degree of maturity, is offered *ad libitum* access to more than one feed, as a choice. Each 'rule' is developed from the interplay between an assertion and a satisfactory experimental test of a given feeding choice. The assertion states, *a priori*, what choice the animal should make if its behaviour is to be consistent with the notion of evolutionary fitness. The experimental data are used to test the validity of the asserted rule.

The types of experiment fall into three classes, corresponding to the three conditions necessary for non-limited growth, namely, that the animal is given

the opportunity to choose:

(a) a diet in which the ratio of nutrient:energy is perfectly balanced.

(b) a diet which is not too bulky.

(c) a diet which is not toxic.

Matters are simplified if each of the three classes of experiment is regarded as essentially a choice between two feeds, rather than between three or more. It is assumed that there is no outcome of relevance to nutrition when the feeds on offer are identical save their position relative to the animal. Thus, the pairs of feeds of interest are those which differ in only one nutritional variable, appropriate to its class (for instance, in the class of choices for a balanced diet one test could be between two feeds of differing protein content). These pairs of feeds then fall into one of three further categories: *non-limiting/non-limiting pairs*; *non-limiting/limiting pairs*; and *limiting/limiting pairs*.

The resultant schema describing all the possible choice-feeding experiments consists of nine categories. These are shown in Table 2.3, where the nutritional variable is given, and the implications for the animal should it choose exclusively only one of the feeds is given in italics. Three of the nine feed pairs are limiting. The remaining six permit a full description of how the animal acquires the resources to express its potential for growth.

2.5.1 Class I. Rules for the Choice of Feed Balance

CHOICE I (i)

Feed A	Feed B
High nutrient: energy	Higher nutrient: energy
non-limiting	*non-limiting*

The animal cannot fail to choose a non-limiting diet, but must take in an excess of nutrients.

RULE 1.

Assertion: The animal seeks to minimise its excess intake of nutrients, and consequently avoids completely the feed with the higher nutrient:energy ratio.

Table 2.3 The Set of *ad libitum* Two-Choice Feeding Experiments

Class I	The Choice of Feed Balance	
Choice	Feed A	Feed B
I (i)	High nutrient:energy *(non-limiting)*	Higher nutrient:energy *(non-limiting)*
I (ii)	High nutrient:energy *(non-limiting)*	Low nutrient:energy *(limiting)*
I (iii)	Low nutrient:energy *(limiting)*	Lower nutrient:energy *(limiting)*

Class II	The Choice of Feed Bulkiness	
Choice	Feed A	Feed B
II (i)	Dense *(non-limiting)*	Denser *(non-limiting)*
II (ii)	Dense *(non-limiting)*	Bulky *(limiting)*
II (iii)	Bulky *(limiting)*	Bulky *(limiting)*

Class III	The Choice of Feed Toxicity	
Choice	Feed A	Feed B
III (i)	Non-toxic *(non-limiting)*	Non-toxic *(non-limiting)*
III (ii)	Non-toxic *(non-limiting)*	Toxic *(limiting)*
III (iii)	Toxic *(limiting)*	More toxic *(limiting)*

Tests: Musten, Peace and Anderson (1974) gave rats continuous *ad libitum* access to two feeds, of similar ME yield, one of which contained 0.40 crude protein (CP) by weight, the other 0.70 CP. Both feeds were demonstrated to exceed the protein requirement of rats, when offered singly to similar test rats. The rats consumed 0.93 of their diet as the 0.40CP feed, thereby coming close to minimising their excess nutrient intake. However, it appears from these data that complete avoidance of excess mutrient intake does not occur. The searching behaviour of animals may lead them to test, periodically, the feeds which they have on offer. Such behaviour allows the animal to remain informed about the feeds which are available (Krebs and McCleery, 1984). This theory may explain the residual intake of the 0.70CP feed by the rats.

CHOICE I (ii)

Feed A	Feed B
High nutrient: energy	Low nutrient: energy
non-limiting	*limiting*

The animal fails to select a non-limiting diet if it eats exclusively feed B. It has an excess nutrient intake if it eats exclusively Feed A.

RULE 2:

Assertion: The animal chooses a non-limiting combination of the two feeds which avoids excess nutrient intake.

Tests: The majority of choice-feeding experiments reported in the literature test the animal's ability to select a non-limiting diet under these conditions. Most authors conclude positively that animals can express their potential for growth given such a choice.

Osborne and Mendel (1918) and Mitchell and Mendel (1921) followed Evvard's lead in the area of choice-feeding, and, working with the rat, concluded that,

> the desire of a young animal for food is something more than the mere satisfaction of calorific needs. The demand made by the growth impulse must be met by a feed of the proper chemical constitution (Osborne and Mendel (1918).

Richter, Holt and Barelare (1938), Leshner, Siegel and Collier (1972) and Musten *et al* (1974) continued the experimental research in this topic and all reported

the ability of the rat to choose a non-limiting diet. Musten *et al* (1974) included a test of the choice made by rats at low and high ambient temperature. The rats demonstrated an ability to choose a balanced diet, the composition of which differed according to temperature. Finally, wild rat species, such as the Norway rat (Griffiths and Harmon, 1954) and Southern Plains wood rat (Harriman, 1974) have also been shown to be experimental subjects capable of discriminating between feeds of different nutritional value.

In poultry, Kempster (1916), Pearl and Fairchild (1921), Rugg (1925) and later Banta (1932), Graham (1932) and Funk (1932) explored the possibility that chickens can choose non-limiting diets when given a wide range of feeds from which to select. Funk concluded that:

> the requirements of the young growing chick and its ability to satisfy these demands can be used to balance a ration if necessary ingredients are available.

Wood-Gush and Kare (1966) and Vohra and Neil (1969) tested the ability of poultry to select an adequate proportion of a given mineral in their diet, when offered a mineral-rich feed and a mineral-deficient feed, as a choice. Vohra and Neil (1969) reported that turkey poults, after two weeks of age, discriminate in favour of zinc-rich feeds as against zinc-deficient feeds. Wood-Gush and Kare (1966) had made similar observations of feeds with calcium as the nutritional variable. More recently, interest in choice-feeding has been rekindled for its potential benefits in intensive poultry production. The papers of Emmans (1977) and Rose and Michie (1982) record the ability of the laying hen and turkey to sustain good production by balancing their diet, when given whole cereal as one of the feed pair and a high-protein 'balancer' as the other. Emmans (1977) pointed out the savings that such a choice-feeding system can make in the protein usage by the flock. Since each individual is permitted to choose a diet suited to its own needs, excess protein intake is minimised if the mineral status of both feeds is adequate. The hens can also balance their diet in relation to any fluctuation in environmental temperature.

Since the initial interest which was shown in the pig as a subject for testing the idea that animals can choose a balanced diet, little work was done until Devilat, Pond and Miller (1970), Jackson, Robinson and Khalaf (1970), Wallace, Palmer, Carpenter, and Coniks (1973) and Robinson (1974, 1975) confirmed Evvard's finding using a number of different experimental designs.

The sheep, however, has rarely been used in controlled-environment choice-feeding studies. More research emphasis has been placed on the diet selection made by sheep in the field (Hodgson, 1982) presumably because such work is considered to be more directly applicable to the sheep industry, in which the majority of lambs are reared outdoors. It is hoped that the rules proposed here, and which are tested against data from controlled-environment experiments, will assist in the interpretation of the choice of diet made by all animals and, in their turn, grazing sheep in the variable environments of the field. Gordon and Tribe (1951) offered six pregnant ewes three feeds (fishmeal, maize and hay, plus a mineral lick) and found that the animals did not select a diet which was adequate to bear or support the number of lambs anticipated. The intention of the experiment had been to overcome the problem of depressed feed intake of ewes in late pregnancy, but as an experimental subject for the testing of the rules of diet selection, the pregnant ewe is not to be recommended. It is possible that the ewes were neither in perfect health, nor in their desired body state, at the beginning of the experiment. The metabolic demands of pregnancy may fluctuate widely, or could have exceeded what the feeds provided. In addition, there were no control treatments in the experiment with which to compare conception and lambing rates of the choice-fed animals.

The weight of the experimental evidence, therefore, supports the idea that animals possess the ability to seek, and distinguish between feeds, in order to choose a non-limiting diet. This simple idea has been tested in a number of ways on many species, and has been a favoured area in the topic of diet selection. The lesser number of contradictions to the theory that animals can choose a non-limiting diet,when given the chance, will be discussed in the closing remarks on the rules of diet selection.

CHOICE I (iii)

Feed A	Feed B
Low nutrient: energy *limiting*	Lower nutrient: energy *limiting*

The animal fails to find an adequate diet from any combination of the two feeds. Therefore, it minimises the deficit in nutrient intake by eating the feed

with the higher nutrient:energy ratio (Feed A). The animal eats as much of this feed as it can lay down as excess fat, or dissipate as heat, up to the point of thermoneutrality.

RULE 3:

Assertion: The animal seeks to minimise its deficit of nutrient intake and therefore shows a complete preference for the feed with the higher nutrient:energy ratio.

Tests: Musten *et al* (1974) offered rats a choice between a protein-free feed (PF) and one of three other limiting feeds (named 5CP, 10CP and 20CP, which correspond to 50gCP/kg, 100gCP/kg and 200gCP/kg respectively). The rats showed a strong but not exclusive preference for the less limiting feed and as previously described in relation to Choice I (i) (the *non-limiting/non-limiting* pairs), the general searching behaviour of nutritionally dissatisfied animals may have been taking place, in that the rats, failing to acquire a non-limiting diet despite showing a preference for the less limiting feed, were motivated to continue to test the other feed available, that is, the PF feed.

Holcombe, Roland, and Harms (1976) report a variable response in hens to such a problem of diet selection. Some individuals chose their diet at random, whilst others, on similar treatments, preferred one of the feeds. The authors attempted to explain these outcomes by means of an intervening learning theory. It is also possible that the feeds were not alike in all nutritional variables except the intended difference in protein content.

2.5.2 Class II. Rules for the Choice of Feed Bulkiness

Experimental evidence with which to test ideas on the choices made by animals between feeds which differ only in their bulkiness is very scarce. Most of the work published in the literature addresses only one dietary selection problem (that of choosing a non-limiting diet in terms of nutrient balance) and in so doing overlooks the dimension of feed bulkiness.

Presumably, this situation has arisen partly from the fact that those animals, to which the selection of a diet from bulky feeds is most commonly a problem,

namely to ruminants, are seldom chosen as the best subjects for controlled-environment experiments. Smaller, simple-stomached animals like rats and chickens are more favoured for indoor experimentation, but are not commonly given bulky, fibrous feeds. Therefore, the outcome of choice-feeding experiments on bulky feeds has usually been measured as the performance of grazing ruminants at pasture, and since determination of feed intake in field conditions remains a major technical problem (Forbes, 1987), data on the diet selection of bulky feeds is sparse. In addition, field trials cannot achieve the necessary control of other nutritional variables (e.g nutrient content) in order to make the choice available to the animal a test in one nutritional dimension.

For these reasons, predictions of the choice for feed bulkiness are difficult to test, and the simplest expectation to take is that the animal will always seek to minimise its bulk intake in order to minimise the time occupied in feeding and digesting (and thereby decrease its supposed exposure to predators) This idea would conform to the view of Krebs and McCleery (1984) that animals seek to maximise their rate of feed intake.

There are no experiments reported in the literature which were designed to test this specific hypothesis in a controlled environment, but the work of Glimp (1971) may be quoted as an example of the behaviour of sheep when offered two, possibly bulk-limiting feeds. The lambs were given a free-choice of four feeds, all of which contained 0.12CP and which included varying proportions of alfalfa hay and corn. All feeds were probably limiting to growth because they contained insufficient protein, but the lambs showed a preference for the higher density feeds. There are two possible reasons for this outcome. The feeds which contained a large proportion of hay had a higher heat increment of feeding and in the high ambient temperatures (up to 33°C) under which the experiment was conducted, could have constrained feed intake by heat stress (a limitation in terms of nutrient balance). On the other hand, the hay-based feeds would also limit growth through their bulkiness, and if this were the cause of constraint, the lambs would make greater gain by feeding on the cereal-based feeds. The actual cause for constraint is not clear, and may have changed during the course of the experiment, but the lambs can be seen to minimise the deficit in their intake of the first limiting resource to growth.

2.5.3 Class III. Rules for the Choice of Feed Toxicity

The difficulty in defining the toxicity of feeds has hindered progress in this area of nutrition research and, consequently, there are few tests reported in the literature of the choice-feeding behaviour of animals given various toxic/non-toxic options.

However, the motivation of animals to avoid toxic feeds, if given the chance, is apparently strong, as the work of Leung, Rogers, and Harper (1968) on rats, Jackson *et al* (1970) and Robinson (1975) on pigs, has amply shown. These workers gave animals a choice between a protein-free feed and another feed totally deficient in one amino acid. Since none of the heavy concentration of amino acids in the deficient feed can be used by the animal, (when the feed lacks completely a certain essential amino acid for tissue synthesis) the deficient feed acts effectively as a mild poison. On eating the deficient feed, the animal must deaminate all the amino acids it consumes. Therefore, Leung and others were actually giving their test animals the choice between a limiting, non-toxic feed (the protein-free) and a limiting, toxic feed (the deficient). They report unanimously that the animals avoid the toxic feed completely.

The schema, thus complete, indicates where it is considered that sufficient work has been carried out to test the appropriate rule, and where it is considered that data are wanting. Furthermore, the approach offers a way to understand the outcomes of more complex choice-feeding situations, for instance, when the animal is obliged to select a diet from two feeds which differ in more than one nutritional dimension. These circumstances tend to obscure the reasons for the animal's choice of diet, a choice which, according to its complexity, may be changeable or defective.

2.5.4 Apparent Contradictions to the Theory

Opponents to the theory of 'nutritional wisdom' in animals hold that animals cannot chose what they need, nor avoid what they do not. Moreover, there is an adequate literature to support this negation. Jordan (1906), Kon (1931), Scott (1946), Scott and Quint (1946), Coppock, Everitt and Merrill (1972), Cowan and Michie (1977) and Pamp, Goodrich and Meiske (1977) concluded that the

animals used in their experiments were not able to select a diet which supported their potential for growth.

These papers are to be valued because few scientists interested in choice-feeding set out with the intention of disproving the theory that animals can select a non-limiting diet. The outcomes of apparently contradictory experiments can therefore be used to define more clearly the nature of choice-feeding behaviour and the conditions which constitute a free choice of feeds.

When studied critically, the experiments which show the failure of animals to select non-limiting diets can be seen to belong to one of two types: those which did not give the animals the necessary choice to choose from, and those which did not give the animals the necessary chance to choose.

The instances of the failure in animals to select a non-limiting diet reported by Kon (1931), Scott (1946) and Cowan and Michie (1977) may be considered to belong to the first category described above, namely those experiments in which the animals may not have been given a choice to choose from. In each of these experiments the animals were given a selection of feeds, the quality of which was not tested independently by feeding them singly in control treatments. Consequently, the idea that the animals were not given a choice from which they could choose a non-limiting diet remains an untested possibility.

The unfortunate omission of control treatments in many published experiments prompts thought as to what may be more properly considered as a complete choice feeding experimental design. Taking the example of Musten, *et al* (1974), who tested the rat's ability to choose a non-limiting diet, when given a protein-free feed (A) and one of five protein-supplemented feeds (B, C, D, E and F), the full experimental programme would have included each of the six feeds fed singly, plus the fifteen combinations of feed pairs. For completeness, each set of treatments would be conducted at a number of different environmental temperatures.

Musten *et al* (1974) employed only a sub-set of these twenty-one treatments, presumably in the interests of economy, but picked the treatments which allowed them to detect shortcomings in the feeds, particularly from the data of the single-feed treatments, before they interpreted the outcomes of the

choice-fed treatments. By means of this design, these workers showed, for example, that rats offered choices of feeds with gluten as the source of protein in the feeds, rather than casein, could not select a non-limiting diet, because both the protein-free feed and the gluten-based feeds were limiting. They concluded this from the evidence that none of the gluten-based feeds, even at extremely high levels of inclusion (0.5 - 0.7 gluten) could support the potential for growth when fed singly.

In the papers which report the failure of animals to select a non-limiting diet, this thoroughness of method is not evident. It is therefore difficult to dismiss the idea that the feeds offered in these cases were not, in a true sense, a free choice.

The argument that animals are often not given a chance to choose a non-limiting diet centres on the problem of defining a 'choice'. Scientists interested in the animal's sense-perception of the feed, through its taste, odour, texture or position, often measure a 'choice' on a short-time scale of minutes or hours, which may not bear a direct relationship to the longer-term nutritional consequences of taking that feed. In such cases, the animal may not have been given an adequate opportunity to choose a non-limiting diet, say, from an unreasonably large number of unidentifiable feeds e.g. individual, inorganic mineral compounds in the case of Coppock *et al* (1972) and Pamp *et al* (1977)] or before the feeds are removed (Pamp *et al*, 1977) and the observations ended (Kenney and Black, 1984). Anecdotal evidence of hungry livestock escaping and overeating when unsupervised or released on to fresh pasture, often used as proof that 'animals don't know what's good for them', are considered to be more a reflection of the unnatural restraint from which the stock have been incautiously released than the animal's inability to choose. In instances such as these, the animals have little opportunity to learn from mistakes which usually prove fatal.

That an animal takes longer than a few days to choose a non-limiting diet, particularly when given novel feeds, is not considered to be sufficient grounds for dismissing the notion of 'nutritional wisdom', in which a delay in response to the nutritional effects of a certain choice may be expected from knowledge of the time-course of digestive and assimilative processes in animals. The idea of free-choice feeding, as used in this chapter, relies on the animal being given continual and undisturbed access to fresh feeds from which it can select

its diet. Studies of the length of time that an animal takes to learn what diet to choose remain within the boundaries which test theories of learning behaviour in animals.

Krebs and McCleery (1984) have criticised experiments in which the animal is tested in 'unnatural' conditions, particularly when the animal is 'tricked' during the making of its choice. During the search for food, animals are believed to use cues such as taste or position of the feed, firstly, as a means of perceiving that the stuff is potentially a feed, and secondly, to help guide them in future searches to whatever stuff had been previously experienced as nutritious. As an example, an animal may use the position of a feed as a cue for returning to that which provides a certain required resource. If the experimenter changes the position of the feed more frequently than the time interval which it takes the animal to learn the consequences of mistakenly choosing the wrong feed (by following the position cue) the animal is 'tricked' or confused, and will fail to choose a diet which matches its requirements. Wood-Gush and Kare (1966) and Vohra and Heil (1969) controlled for position effects by relocating the feeds on offer apparently too often for the animals to realise the nutritional consequences of following a positional cue. Studies of the use of cues and other learning behaviour have their rightful place in animal science but it is important to see them in proper relation to longer-term theories based on considerations of the growth aims and nutritional requirements of the animal.

Furthermore, speculation about the use of odour or taste as a cue for finding feeds is appropriate at the level of feeding behaviour, but if the theory is extended to the prediction of all feeding choices made by animals, it is found to fail upon rigorous testing, such as when the animal is faced with serious nutritional decisions. For example, Blair and FitzSimons (1970) sought to limit feed intake in a group of pigs offered *ad libitum* access to single feeds impregnated with differing levels of 'Bitrex...the bitterest substance known to man'. Their theory was that animals do not like bitter feeds, and will therefore decrease their feed intake when given such feeds. It is possible that, initially, the pigs avoided such repugnant stuff as the Bitrex-impregnated feed because they had previously learned to associate bitter odours or tastes with the harmfulness of a toxin. Later, however, on discovering that there was no other feed available, and that eating the bitter feed did not bring about a toxic effect, their hunger would overpower the misleading sensory cue, and they would eat

the feed. Blair and FitzSimons (1970) reported that there were no significant differences in feed intake between the untreated and treated feed groups and came to the conclusion that the pigs could not detect Bitrex.

In the case of Blair and FitzSimons, the taste or odour of the feed, (factors which contribute to the quality known as feed palatability or acceptability) became unimportant to the animal when the consequences of avoiding a feed, on the basis on an untested sensory assumption, were great. It follows that an animal given a choice of feeds will, in the long-term, desist from eating the tasty feed (or what the scientist imagines is the tasty feed), if that feed does not provide the first limiting resource which the animal requires to satisfy the specifications of the growth-plan. Palatability studies are therefore only of use in testing theories of animal perception and have little to contribute to the understanding of diet selection made by the animal on the basis of what has been presented as a nutritional theory of the animal's behaviour. At this point, therefore, it is important to make the distinction between the nature of palatability and that of toxicity in feeds. Palatability, if it is measurable, has been demonstrated to have, at most, a fleeting influence on feeding behaviour which is subservient to the nutritional concerns of the animal. Toxicity, though difficult to quantify, is to be regarded as a distinct, if commonly correlated, characteristic of feeds which has a direct bearing on the feed intake of the animal.

2.5.5 A Preliminary Evaluation of Choice-feeding

Thus, it has been proposed that there are two principal causes for the reported outcomes that animals did not choose non-limiting diets. Moreover, the review of the literature in choice-feeding has indicated that the weight of evidence lies in favour of the idea that animals select their diets, in a wide range of circumstances, according to what have been styled 'rules' for optimising their feeding strategy. Several of the tested combinations of feeds have shown features which suggest that the technique of choice-feeding is a useful alternative to the more established methods of providing animals with the best possible conditions for growth. In relation to ruminants, it is remarkable that so few experiments have been conducted under controlled environmental conditions on either sheep or cattle. Consequently, the remainder of this chapter reports the findings of three experiments designed to

test some of the asserted 'Rules of Diet Selection' in order to assess the usefulness of the approach to defining non-limiting conditions for the growth of sheep.

2.6 Experiment 1: A Test of the Rules for the Choice of Feed Balance by Growing Lambs

2.6.1 Objectives

The experiment was undertaken to test ideas on diet selection and then to assess their validity as descriptors of both the behaviour, and the conditions which are non-limiting for the growth, of sheep. Each lamb was to be given free and continual access to two feeds which differed, as far as is practically possible, in only one nutritional variable. The variable chosen for this preliminary investigation was that of protein: energy ratio since this was thought to be a factor of major importance to the animal and was simple to implement.

2.6.2 Propositions

Consequently, the set of propositions to be tested by experiment which corresponded to the Rules of Diet Selection outlined in section 2.5 of the review, were:

P1: lambs will choose between the feeds on offer in a directed (non-random) manner.

P2: lambs will not select their diet on the basis of the position of the feeds.

P3: lambs will minimise an excess of protein intake.

P4: lambs will select a diet of a certain composition, according to the protein content of the feeds on offer, at a given degree of maturity.

P5: the protein content of the diet selected will decrease as the lambs mature.

2.6.2.1 Corollaries

Should propositions P1-P5 survive, the theory predicts that the lambs will select a nutrient: energy balance in their diet such that energy is the first

limiting resource for growth. Under these circumstances, all the lambs will:

C1: have a similar daily rate of total feed intake which is dependent on, and predictable from, their energy requirement for maintenance, growth and fattening.

C2: grow at a rate set by their inheritance i.e. they will achieve their potential rate of growth.

2.6.3 Materials and Methods

Animals Twelve Suffolk X Greyface (SGF) wethers, reared as twins on their mothers, were selected from an experimental farm flock on the basis of growth rate from birth. At a mean age of 62 (s.d. 5) days the lambs weighed 24.6 (s.d. 0.5)kg liveweight (LW), were group penned and were weaned on the hay and one of the experimental pelleted feeds which contained (160g CP/kg D.M.). The experiment began eight days later when the lambs weighed 24.9 (s.d. 1.8)kg LW

Feeds Four pelleted feeds were required, with a range of crude protein (CP) contents, but similar yields of metabolisable energy, and similar mineral/vitamin profiles. Initially, two basal feeds were made, one with a low CP content, the other high. Pelleted feeds were favoured because they avoid the problem of selective feeding by sheep given heterogeneous feeds (Moore and Polling, 1961).

The low protein feed (A) was formulated to be inadequate in protein to support potential growth when offered singly *ad libitum* (ARC, 1984). Barley and sugar beet pulp were chosen as the two major components of the feed. The second basal feed (D) was made with a higher CP content intended to be above the requirement of the lambs by substituting soya bean meal for 0.368 of the barley in feed (A).

Since the experiment aimed to test ideas concerning a lamb's selection for protein, it was necessary to equalise the mineral and vitamin contents, as far as possible in feeds A and D, so that these nutrients were present in abundance and in similar relative amounts. Feeds A and D were made accordingly. (See Table 2.4). Four feeds, with a range of CP contents, could

then be made from mixtures of the basal feeds A and D. Feed B was made from 0.37A and 0.63D. Feed C was a mixture of 0.22A and 0.78D. Feeds B, C and D were pelleted individually, and analysed for dry matter and nitrogen, ash fibre, and ether extract in the dry matter. The chemical analysis of the feeds is shown in Table 2.5.

A dilution series of feeds such as this has a number of advantages over the mixing of individual feeds. Feed formulation is simplified to that of the two basal feeds, and, when the feeds differ in only one nutritional variable (in this case CP) any range of feeds, between the two extremes, can be mixed simply by proportion. Errors in formulation, or mixing (for instance complete omission of a necessary nutrient) are more easily detected, since they will show their effect across the entire experiment, and the confusion of "odd" treatments, caused by a mistake in the making of one feed, will be lessened.

Design A complete two-way choice-feeding experiment, using four feeds, comprises of ten treatments, that is, the four feeds fed singly, as controls (treatments A, B, C and D) and the four feeds fed as two-way choices (Treatments AB, AC, AD, BC, BD, and CD). Ideally, the opportunity to assess body composition changes by serial slaughter or energy balance would also be taken.

Unfortunately the experimental resources available were limited to twelve lambs, and, hence, it was only possible to include those treatments considered essential for testing the key propositions of the Rules of Diet Selection. The three treatments chosen were those in which feed A was paired with every other feed, namely A with B, A with C and A with D. A Latin Square cross-over design was employed to permit a test of residual effects between periods. The experiment was therefore divided into three periods (Period I, 4 weeks; Period II, 4 weeks; Period III, 2 weeks.)[8] Each lamb received each feed pair but only in one of the six sequences. There were two replicates of the six sequences (See Table 2.6). The two replicates were selected on the basis of liveweight. Six lambs weighed close to 25kg LW at 25.5 (s.d. 0.2)kg and were allocated at random to replicate 1. The remaining six lambs weighed from 20.7 to 27.1kg LW, and were put in replicate 2 [mean LW 24.3 (s.d.2.4)kg].

[8] This was because the food ran out.

Table 2.4 The Composition of the Basal Feeds (g/kg freshweight) in Experiment 1

Ingredient	Feed A	Feed D
Sugar Beet Pulp	470	470
Ground Barley	470	102
Soya bean meal	0	368
Dicalcium phosphate	5.4	0
Ground limestone	3.1	4.1
Salt	1.3	0.9
BP 160 trace element and vitamin mix	2.3	2.3
Molasses	47.9	52.7
	1000.0	1000.0

Table 2.5 The Chemical Analysis of the Feeds (g/kg freshweight) in Experiment 1

	Feed			
Component	A	B (0.37A + 0.63D)	C (0.22A + 0.78D)	D
Crude protein (CP)	87	160	175	193
Crude fibre	88	102	113	106
Ether extract	12	12	11	13
Ash	61	68	71	72
Dry matter	876	883	881	880
Metabolisable energy[a] (MJ/kg)	10.8	10.5	10.3	10.4
Digestible CP[b]	70	128	140	154

a, b values calculated from feed tables

DCP depends on level of feeding?

Table 2.6 The Design of Experiment 1

Each lamb was offered continuous *ad libitum* access to both feed A and to either B, C or D, in one of six sequences:

Lamb Identity		Sequence	Period			
Replicate 1	Replicate 2		I	II	III	
2	8	1	B	C	D	
6	11	2	C	D	B	Square
1	9	3	D	B	C	I
5	7	4	B	D	C	
4	10	5	C	B	D	Square
3	12	6	D	C	B	II

Table 2.7 The Effect of Treatment on the Proportion of the Total Feed Intake (TFI) taken from the trough which contained feed A (p.feed A, g/kg TFI)

p.feed A (*s.e.*)	Period			Feed Pair mean
	I	II	III	
Feed Pair				
A with B	256 (*139*)	306 (*158*)	255 (*60*)	272 (*67*)
A with C	277 (*107*)	294 (*99*)	507 (*115*)	359 (*64*)
A with D	145 (*31*)	178 (*62*)	595 (*143*)	306 (*78*)
Period mean	225 (*57*)	259 (*62*)	452 (*73*)	312 (*40*)

It was possible to test the proposition that lambs will not select their diet on the basis of the position of the feeds by switching the position of feed A, on two occasions, that is, at the end of the first period and at the end of the second. The position of feed A at the beginning of the experiment was randomised across animals.

Management Each lamb was individually housed in a wire cage set above the floor. Each cage had two identical metal troughs at the front, and a water bucket at the rear. The experimental house had natural ventilation and continuous lighting from fluorescent lamps. The liveweight of the lambs was recorded weekly at 1100h on a Gascoigne, Gush and Dent mechanical weigh crate (100kg X 0.5kg). The feed intake of both feeds was recorded for each lamb daily at 1000h on a Suprema R5 weighing platform (15kg X 5g). Spillage losses for each individual were swept up from the floor, weighed and the value deducted from the calculated daily intake. Refusals were analysed for dry matter whenever there was evidence of dampening by saliva from the lambs. Fresh feed was placed in the troughs after weighing of the refusals so as to offer the lamb equal quantities of both feeds throughout the day. The feeds were completely replaced each week to prevent the possibility of undetected spoilage.

2.6.4 Results

The results are presented in the form of a series of statistical tests, chosen at each point to be the stiffest challenge to the propositions which the design will permit. The actual weekly liveweights and weekly feed intakes for all twelve sheep can be found in Appendix B. A preliminary analysis of the main factors in the Latin Square design of the experiment, according to the method of Cochran and Cox (1950), showed that there were no significant residual effects of treatments between periods. It was therefore permissible to proceed with the analysis of the main effects in the experimental outcomes.

A simple description of the composition of the diet selected, common to the three treatments, is the proportion of the total feed intake (TFI) which was taken from the trough containing feed A, from now on referred to as p.feed A. The period and treatment means of p.feed A are given in Table 2.7.

P1: The expectation that lambs would select a diet in a directed manner

was tested by comparing the null hypothesis (i.e. p.feed A = 500g/kg TFI) against the p.feed A data reported in Table 2.7. In period I (225, s.e. 57) and period II (259, s.e. 62) and over the whole experiment (312, s.e. 40), p.feed A differed significantly ($p < 0.05$) from p.feed A = 500.

P2: The data used for testing proposition (P2), that the lambs would not select their diet on the basis of the position of the feeds, were the p.feed A values recorded for the day preceeding the switching of the troughs at the end of periods I and II, and the p.feed A values for the day following the changeover.

Comparison of the mean value for p.feed A (after) and p.feed A (before), as a test of proposition (P2), would be ambiguous since each individual lamb could fail to eat a similar p.feed A (after) without affecting the mean p.feed A for the group. Consequently, the best test of the proposition was a visual appraisal of the data presented graphically in Fig. 2.1 where it can be seen that on only four occasions, from 24 (2 X 12) recorded, individuals appeared to select their diet on the basis of its position.

P3: Since the idea that a lamb minimises its excess of protein intake can only be tested when it is known, independently, exactly what the requirement for protein is, the design of the experiment did not permit a formal analysis of proposition (P3). However, whilst it has already been shown that p.feed A was not 500g/kg TFI, the data in Table 2.7 also indicate that p.feed A was significantly different from 1000 ($p < 0.001$) and from zero ($p < 0.001$).

P4: The method of formulation of the three feeds of higher CP content (feeds B, C and D) permitted a test of hypothesis P4, that the lambs would select a diet of a certain composition. If all the lambs were to select a diet of a similar composition, the lambs offered feed B with feed A would have to select a lower p.feed A than those offered feed C with feed A. By the same arithmetic argument, lambs offered feed D with feed A would have to select the highest p.feed A.

Proposition P4 was tested by an analysis of the variance of the treatment values reported in Table 2.7. The effect of the treatment of p.feed A was not significant ($p > 0.1$). All the means were subject to wide variation and the values of p.feed A for the lambs of treatment 3 tended to be lower than the other treatments. However, the proposition that lambs select a diet of the same

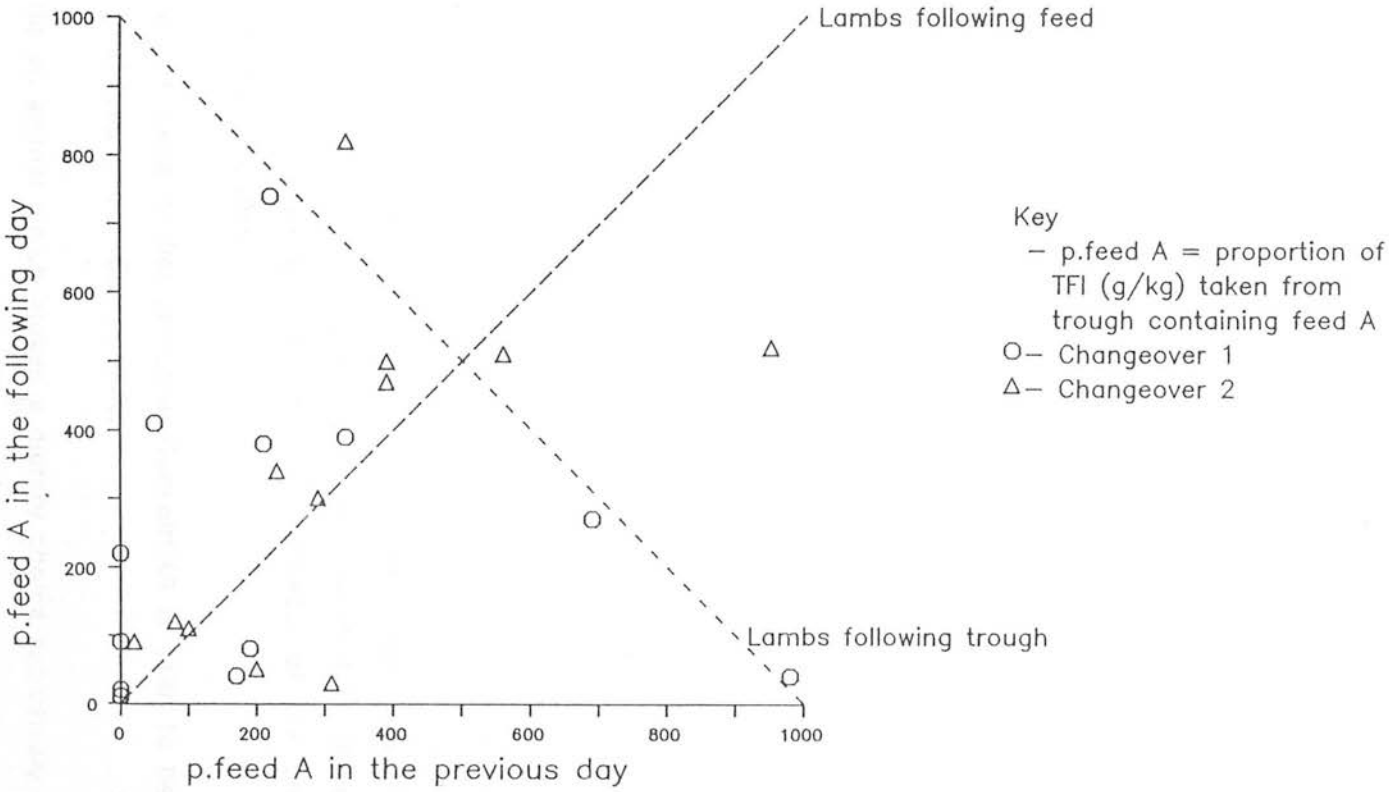


Fig. 2.1 The Effect of a Reversal in the Position of Two Different Feeds on Diet Selection in Lambs

crude protein content still had to be rejected.

P5: The mean period values for the composition of the diet selected provide the data for testing proposition (P5), that the CP content of the diet selected would decrease as the lambs matured.

In relation to the feeds offered, the testable expectation was that feed A increased significantly with period. A comparison of the values for periods I and II showed that the hypothesis was not tenable at the 25% significance level over this time-span. However, when the values for periods I and II were pooled (242, s.e. 41) and compared by t-test with the values for period III (452, s.e. 73), p.feed A was found to increase significantly ($p < 0.05$) with time, which outcome agreed with the expectation of proposition (P5). The decline in the CP content of the diet selected is illustrated in Fig. 2.2.

The analysis of the diet selection data has given no grounds on which to reject propositions (P1 and P5) but has left obscure the more exacting proposition (P4). The opportunity is now taken to exhibit several individual paths of diet selection as typical illustrations of several features of interest in diet selection.

The uniqueness of each lamb's path of diet selection, in a two-way choice feeding situation, is best traced by first calculating the differences in the cumulative intake of feed A and the cumulative intake of the other feed, B, C or D, giving Cum.diff.BA, Cum.diff.CA and Cum.diff.DA. These values are plotted against the cumulative total feed intake Cum.tot.BA, Cum.tot.CA and Cum.tot.DA respectively. The graph of these values, which are orthogonal (see Fig. 2.3), permits the following, more pertinent aspects of the diet selection, to be surveyed at a glance:

(i) the trend in diet selection Cum.diff.XA is seen to be related directly to the total feed intake (Cum.tot.XA).

(ii) an animal which makes a dietary choice exclusively in favour of one of the feeds traces a path [Cum.diff.XA = Cum.tot.XA or Cum.diff.XA = -(Cum.tot.XA)].

(iii) the angle of the plotted path reflects the relative proportions of the two feeds in the diet selected. (i.e when Cum.diff.XA = 0 then p.feed A = 500g/kg TFI).

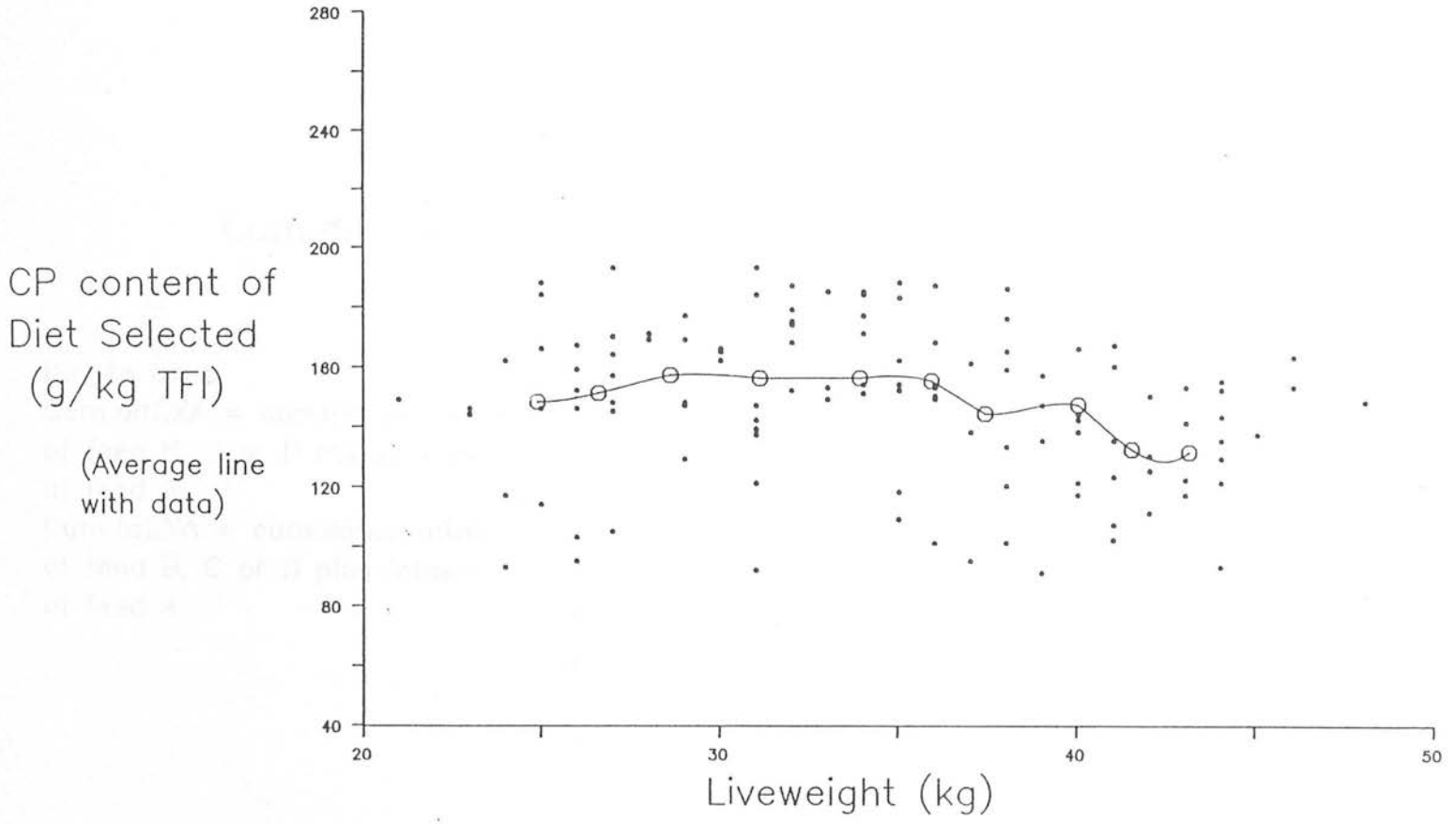


Fig. 2.2 The Crude Protein (CP) Content of the Diet Selected by Growing Lambs

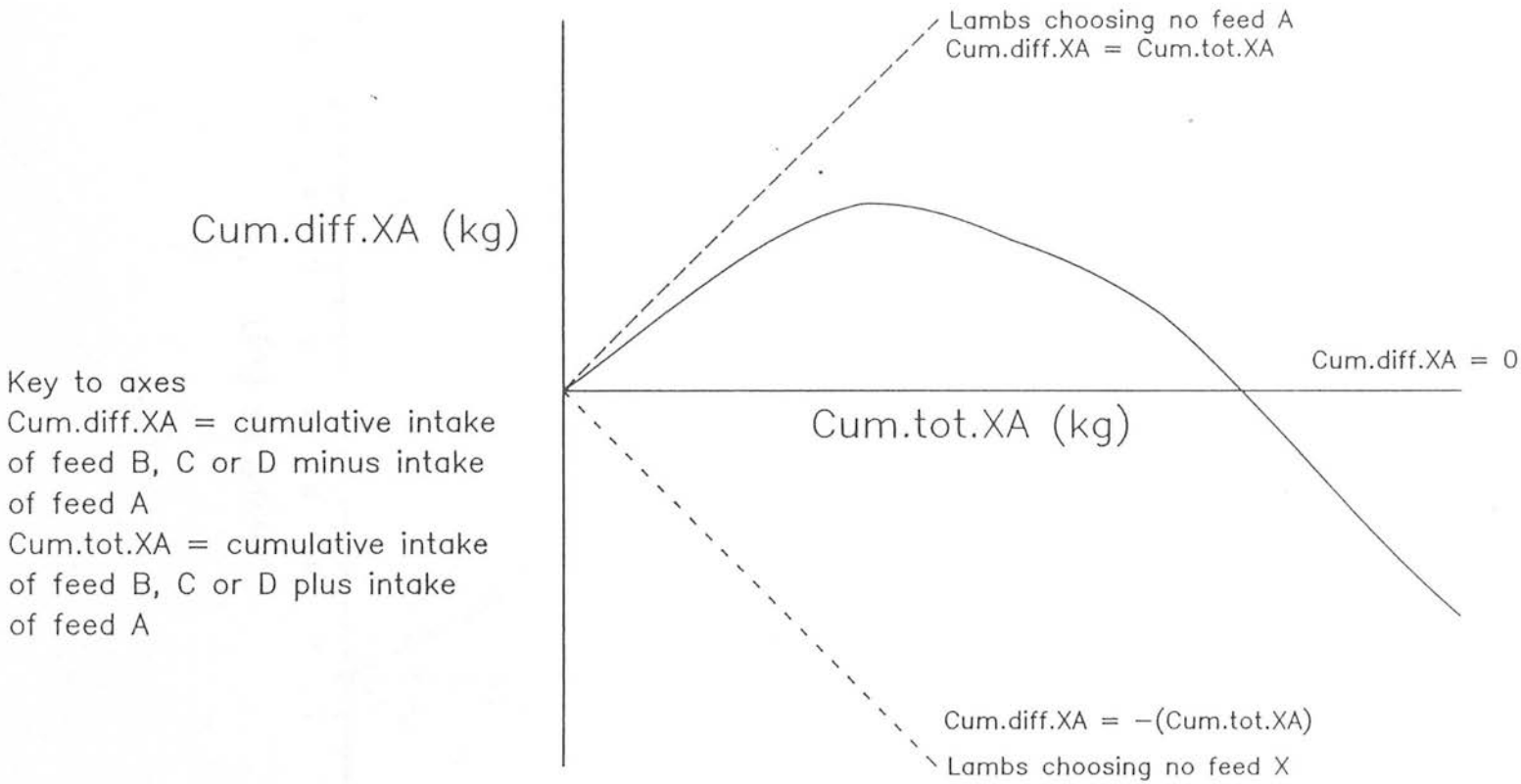


Fig. 2.3 Paths of Diet Selection in Growing Lambs (i) (The Idealised Path)

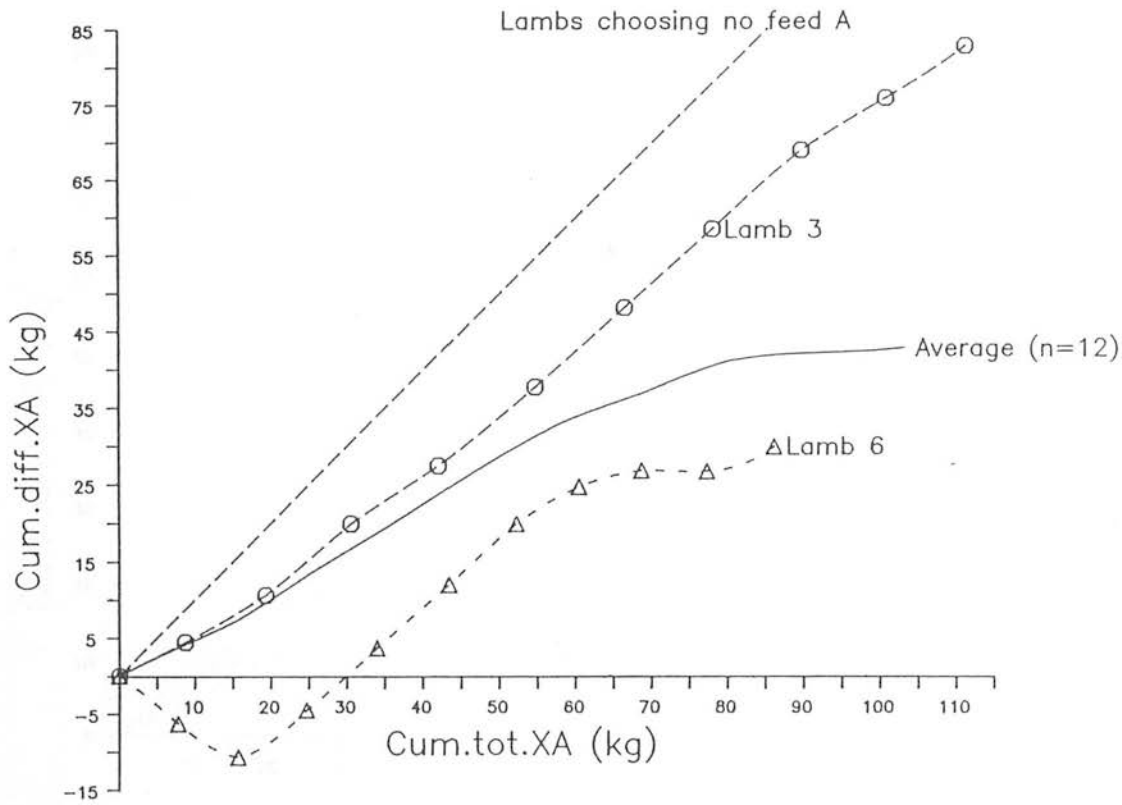


Fig. 2.4 Paths of Diet Selection in Growing Lambs (ii)

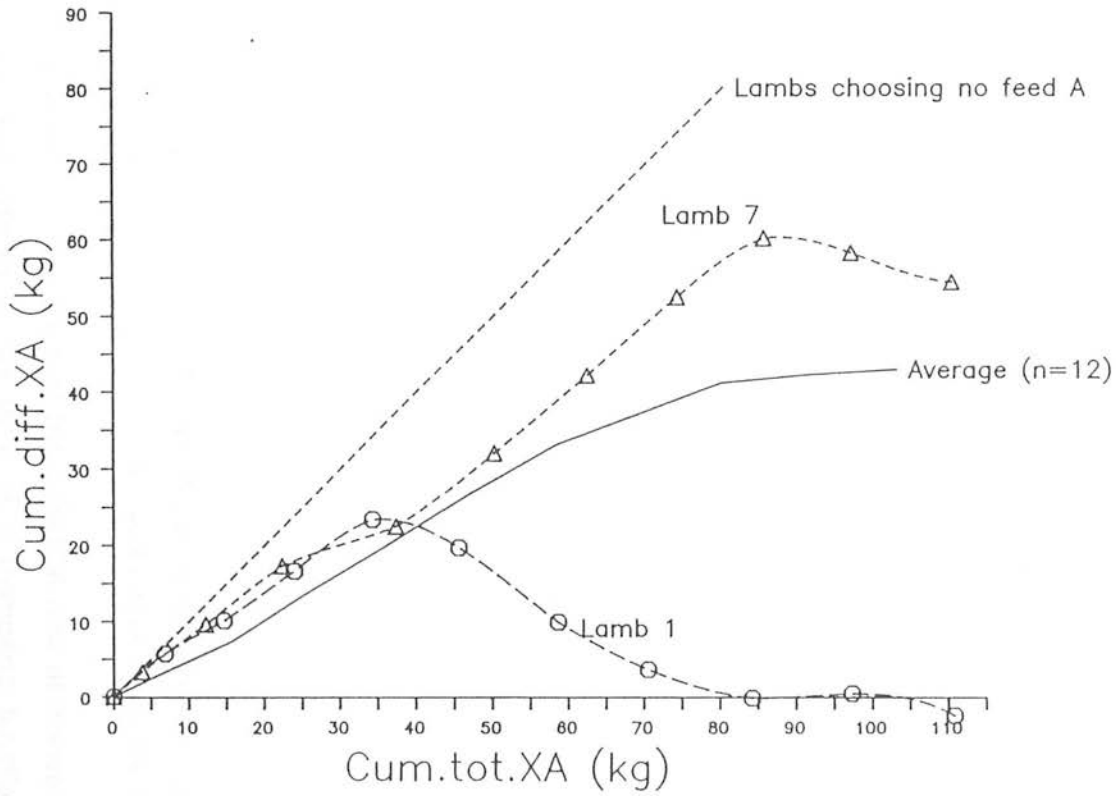


Fig. 2.5 Paths of Diet Selection in Growing Lambs (iii)

(iv) freak, short-term changes in diet composition, disruptive to other plotting techniques (eg p.feed A against time) are smoothed out and the progress of an individual can be traced as it moves through all the possible combinations of the feeds on its way to the mature diet composition (Fig. 2.3). The individual graphs of lamb numbers 1, 3, 6 and 7 are given in Figs. 2.4 and 2.5 and will be referred to in the discussion.

C1: That the daily rate of total intake would not differ between treatments was tested by analysis of a variance; the absence of significant ($p > 0.1$) treatment effects was not different from this expectation.

The plot of rate of TFI against time (Fig. 2.6), showing the significant ($p < 0.01$) period effect found in the analysis of variance, was then compared with two predicted curves. The models chosen for predicting rate of TFI (dF/dt) were

(i) the ARC (1984) prediction (Chapter 2, p. 60)

$dF/dt\ (g/kg\ LW^{0.75}) = (150.3 - 78q - 0.408\ LW)/DMC$

where DMC = dry matter content of feed (measured as 0.88)

q = metabolisability of the feed (calculated as 0.69)

LW = liveweight (measured in the experiment)

(ii) the prediction equation of Emmans (1987,1988) where dF/dt is a function of the energy requirement for maintenance, growth and fattening.

The data deviated systematically from both models which, however, predicted the observed increase in rate of feed intake over the experiment.

C2: In Chapter I a description of the potential rate of liveweight gain in SGF wethers had been offered in the form of a Gompertz function. To make an estimate of the Gompertz rate parameter, B, for each animal in this experiment, the initial and final liveweights were transformed to G_o and G_f respectively using an estimate of mature liveweight of 100kg, so that

$B = (G_f - G_o)/t$

where t = time from the start of the experiment (70 days).

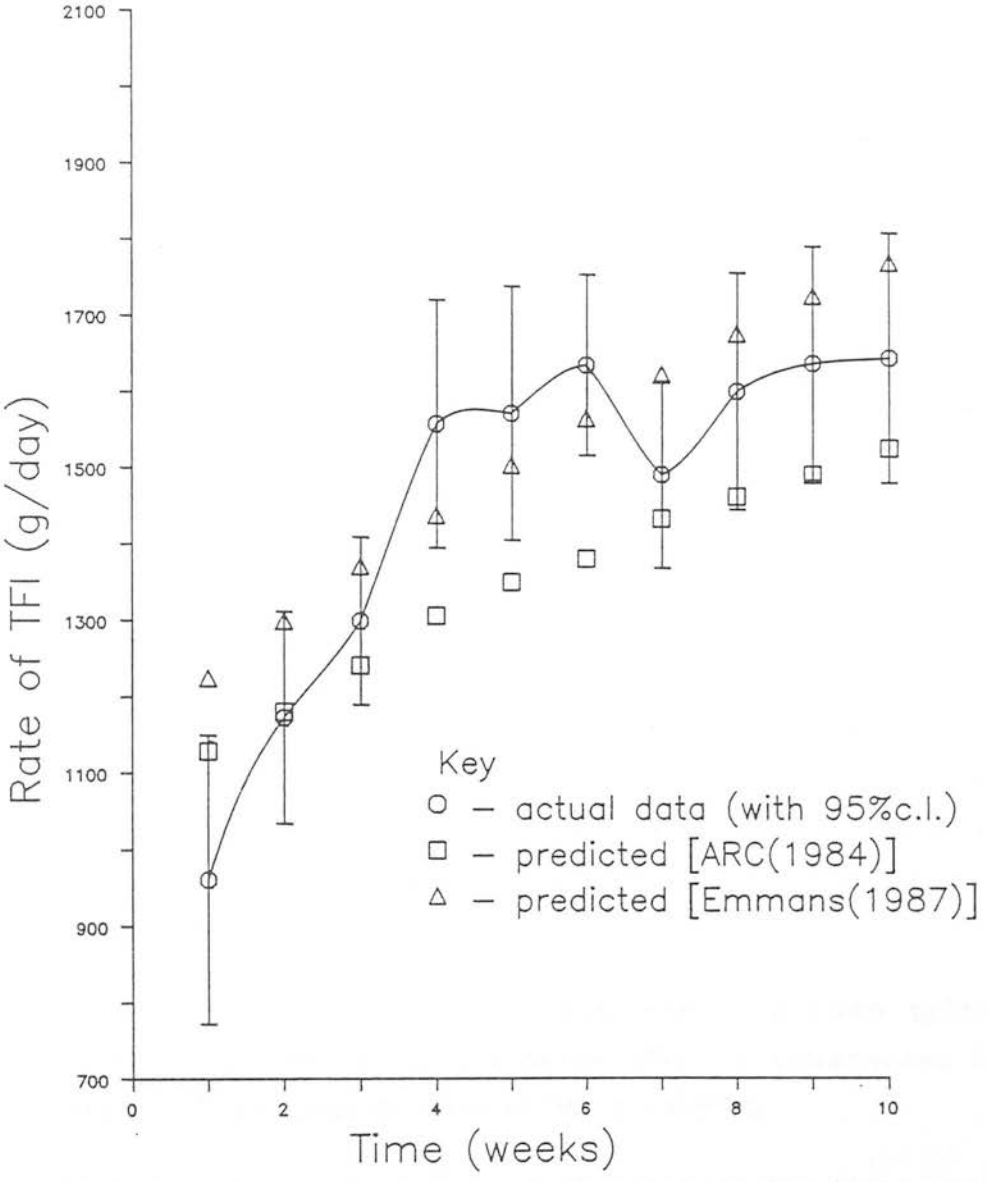


Fig. 2.6 The Rate of Total Feed Intake (TFI) of Choice–fed Lambs

There were no significant ($p > 0.1$) treatment differences and the average B value for the twelve lambs of 0.0079 (s.e. 0.0003) was not significantly different ($p > 0.1$) from the expected value (0.0078) for SGF wethers growing at their potential rate (Chap. I).

2.6.5 Discussion

Reflection on the outcome of the test of proposition (P4), that lambs will select a diet of a certain composition, has brought criticism of the experimental design and the expectations that were held concerning diet selection in sheep.

The lambs chose a diet with a CP content on average of 147 (s.e. 3.3) gCP/kg, which composition was shown to significantly decrease (P4) as the lambs matured (Fig. 2.2). This value was close to that recommended as the requirement (153g CP/kg) for lambs of medium mature size (115kg), eating and growing at similar rates (NRC, 1985). However, by way of the relative closeness of the CP content of the selected diet to that of the three, similar high CP content feeds (feed B, 160g CP/kg, feed C, 175g CP/kg and feed D, 193g CP/kg), it can be seen by arithmetic argument that small differences between individuals in their required CP intake would result in a large variation between treatments in p.feed A. Thus, it may be deduced that the planned differences in the CP content of feeds B, C and D were insufficiently wide to permit the effect of treatment to be an unequivocal test of proposition (P4).

The conditions under which this variation arose and which spoiled the simplicity of the expectations in proposition (P4), are characterised by the individual paths of diet selection given in Figs. 2.4 and 2.5.

In the first instance, Lamb 6 (Fig. 2.4) illustrated the fact that animals can make a defective (i.e limiting) dietary choice when they have had no previous experience of the feeds on offer. Lamb 6 changed the path of its dietary preference for feed A after two weeks and resumed a path similar to that favoured, on the average, by its counterparts. Such a pattern of choice induced variation between individuals, particularly in the early part of the experiment.

Lamb 3 (Fig. 2.4) typified the animal which has an apparently high

requirement for a feed resource other than energy, and in this case, presumed to be protein. Lamb 3 continued to favour the high CP content feeds well after the point where its counterparts began to select a greater p.feed A in the diet. Had the experiment lasted longer, Lamb 3 would be expected to choose a greater p.feed A in its diet, as its requirement for protein relative to energy fell and it sought to maintain an ideal nutrient: energy balance. A downward trend in the plot in Fig. 2.4 would then be observed. This gradual change in diet selection was found in the paths of Lambs 1 and 7 (Fig. 2.5). Lamb 1 began to favour feed A after only 35kg TFI, whilst Lamb 7 shifted its choice after 85kg TFI.

It is proposed that the path of diet selection of every lambs lies on a universal curve of a form common to that of Lambs 1 and 7 but which differs in magnitude for individuals according to their unique requirements for energy relative to protein (see Fig. 2.3). Consequently a high degree of variation may have to be tolerated in both the dimensions of diet composition Cum.diff.XA and total feed intake (Cum.tot.XA) in experiments of this kind, as the individual seeks to express its unique potential. The position could be helped by using more exacting criteria for selecting test animals. More similar initial liveweights and more uniform genetic background for the lambs would be favourable. Another suggested improvement to design, which would allow a more critical test of proposition (P4), would be to formulate the high CP content feeds with a greater difference in their value to the animals. It is recommended that feeds B, C and D span a wider range in CP content than was employed in this experiment.

2.6.6 Conclusions

The data collected in this experiment have supported several of the assertions arising from the Rules of Diet Selection (2.5). It is therefore concluded that the lambs selected a diet:

(a) in a directed manner.

(b) independently of feed position.

(c) which avoided excess protein intake.

(d) which changed as they grew.

(e) which was not first limiting in a nutrient. Since the feeds on offer were both highly digestible and believed to be non-toxic, it was evident that the lambs had achieved the non-limiting conditions for growth, as defined in section 2.3.

(f) which supported their potential for growth.

2.7 Experiment 2: A Second Test of the Rules for the Choice of Feed Balance

2.7.1 Objectives

This experiment was conducted to test more severely the theory that growing sheep can select a diet adequate to support their potential growth, a theory which carried an implicit definition of the non-limiting conditions required by the sheep to fulfill its inherited growth-plan.

The elected approach to the problem included similar sheep and had the same outline as Experiment 1 (Exp.1). The further advantage to this strategy was that the outcomes of Exp.1 could be used as a basis for firmer expectations in this experiment.

The lambs were offered a free choice between two feeds, one insufficient in crude protein (CP) to support the supposed potential for growth, the other super-adequate. In this experiment, however, the range of CP contents of the super-adequate feeds was broadened. This modification in design came in response to the weaknesses in method encountered in Exp.1.

Furthermore, it was considered that the experience gained from Exp.1 removed the necessity to test the effect of changing the feed position and the effect of the sequence of the feed pairs, since the data obtained in conjunction with the Latin square design of Exp.1 had shown these aspects of the theory to be of minor importance. It was felt that more resources could be placed into establishing the response of lambs when given free access to single feeds and also to testing, in its own right, the proposition that lambs will minimise their excess protein intake.

Therefore, the fundamental proposition of the theory, which had survived the challenge of Exp.1, were asserted once again.

2.7.2 Propositions

P1: lambs will select a diet in a directed manner.

P2: lambs will minimise their excess of nutrient intake.

P3: lambs will select a diet with a similar composition. The gross average CP content of the diet selected, during the first ten weeks from 25kg LW, will be 147g/kg TFI and will fall throughout the ten weeks.

2.7.2.1 Corollaries

Should all the lambs select a common diet, their growth will not be first limited by a nutrient, in which case, the following corollaries apply:

C1: all the choice-fed lambs will have a similar TFI. From a liveweight of 25kg, the rate of TFI will have an average value of 1248g/day within the first four weeks. The rate of TFI will increase after the first four weeks. The overall TFI for ten weeks from 25kg LW will be 102.1kg.

C2: lambs offered a single feed, super-adequate in CP, will have similar TFI characteristics to choice-fed lambs.

C3: lambs offered a single feed, deficient in CP, will initially raise their rate of TFI above that of choice-fed lambs in order to attain their desired intake of protein.

C4: all choice-fed lambs will have a similar Gompertz liveweight gain rate parameter, B, expected to be (from Exp. 1) 0.0078.

C5: lambs offered a single feed, super-adequate in CP, will have a similar B value to choice-fed lambs.

C6: lambs offered a single feed, deficient in CP, will remain limited in protein intake and hence will fail to achieve the growth rates of choice-fed animals.

2.7.3 Materials and Methods

Animals Twenty-four Suffolk X Greyface wethers (n = 12) and females (n = 12) at an approximate age of seven weeks and 19.6 (s.d 2.1)kg liveweight, were purchased from a commercial farm where they had been artificially reared from birth on milk substitute and then weaned onto a barley-based feed with hay.

Feeds Four pelleted feeds were used and were made with a range of CP contents by the dilution method described in Exp.1. The two basal feeds were mixed first. The low protein feed A' was of the same formulation as feed A in Exp.1 with some small alterations to the mineral supplement. White fishmeal was chosen as the protein source in the high protein basal feed D' because it had a suitably high CP content to permit a wide range of CP contents in the choices offered. Thus, feed D' contained 0.57 fishmeal which replaced 0.47 barley and 0.10 sugar beet pulp in feed A'. The composition of feeds A' and D' are given in Table 2.8. The range of four CP feeds was made from mixtures of feeds A' and D'. Feed B' was a mixture of 2/3 A' and 1/3 D'. Feed C' was made from 1/3 A' and 2/3 D'. A proximate analysis of the feeds was carried out and the results are given in Table 2.9.

Design The twenty-four lambs were allocated to six treatments. In order to balance for weight and sex, the pool of lambs was divided into two weight categories within each sex. Each treatment then received two 'small' and two 'large' lambs, one from each sex. The main experimental treatments lasted for ten weeks, unless otherwise stated, and the design of the experiment is given in Table 2.10.

Management The housing and penning facilities were identical to those described in Exp.1. Liveweight and feed intake was recorded weekly for ten weeks. Treatment 6 was discontinued after four weeks (see Results). The experimental resources available permitted treatment 1 to be continued for a total of twenty-one weeks. Liveweight was recorded weekly on a Bizerba MCI 400 Electronic weighing platform (150kg X 5g divisions). The weighing procedure began at 11.30 am and followed the same animal sequence each week. The lambs were given fresh feed daily. The feed routine began at 9.00h daily and also followed the same animal sequence. Feed refusals were weighed weekly on a Suprema R5 weighing platform (15kg X 5g) and discarded. Refusals were analysed for dry matter content, and the apparent feed intake adjusted, if there was evidence of dampening by saliva from the lambs. Spoiled feed was recorded and discarded during the week when the occasion arose. Spillage losses for individuals were also recorded.

Table 2.8 The Composition of the Basal Feeds (g/kg freshweight) in Experiment 2

Ingredient	Feed A'	Feed D'
Sugar beet pulp	470	380
Ground barley	470	0
White fishmeal	0	570
Dicalcium phosphate	5.7	0
Ground limestone	3.3	0
Salt	1.5	1.5
Nutrikem sheep trace element/vitamin mix	2.5	2.5
Molasses	47	46
Total	1000	1000

Table 2.9 The Chemical Analysis of the Feeds (g/kg freshweight) in Experiment 2

Constituent	A'	B' ($\frac{2}{3}$A' + $\frac{1}{3}$D')	C' ($\frac{1}{3}$A' + $\frac{2}{3}$D')	D'
Crude protein (CP)	91	182	266	383
Crude fibre	82	79	68	60
Ether extract	12	23	37	51
Ash	73	96	122	142
Dry matter	884	878	893	899
Metabolisable energy[a] (MJ/kg)	11.1	11.3	11.7	12.2
In vitro organic matter digestibility	0.89	0.90	0.90	0.90

[a] value calculated from feed tables

Table 2.10 The Design of Experiment 2

Each lamb was offered continuous *ad libitum* access to one or two feeds:

Treatment	Feed 1	Feed 2	n	Duration (weeks)
1	A	B	4	10 [+11][a]
2	A	C	4	10
3	A	D	4	10
4	B	D	4	4[b]
5	B	-	4	10
6	A	-	4	10

a Treatment 1 continued for extra 11 weeks.

b Treatment 4 ended after 4 weeks (see Results)

Table 2.11 The Effect of Treatment on the Proportion of the Total Feed Intake (TFI) taken from the trough which contained feed D' (p.feed D', g/kg TFI)

Treatment	Feed 1	Feed 2	p.feed D' (*s.e.*)	transformed p.feed D' (*s.e.*)
4	B	D	40[a] (19)	105[b] (28)
3	A	D	136 (21)	328 (60)
Difference			96[c] (23)	223[d] (93)

a test for proportion = 0; no significant difference ($p>0.1$)

b test for proportion = 0; significant difference ($p<0.05$)

c significant difference ($p<0.01$)

d non-significant difference ($p>0.1$)

2.7.4 Results

The experiment has been divided into two periods (Period 1, week 1-4; Period 2, weeks 4-10) in order to assist in the analysis of those effects expected to be dependent on the degree of maturity of the animals. The mean values from the six treatments are presented for both periods and the total experiment. The actual weekly feed intakes and liveweights of individual lambs can be found in Appendix C. Lamb 45, on treatment 5, died in week 9. Its data have been excluded from the analysis. Lamb 4 on treatment 1 died in week 15. Its data are included in all analyses until week 10.

As in Exp.1, the data of diet selection are described by the proportions of the total feed intake (TFI) which was taken from the trough containing feed A', written from now on as p.feed A'. Where indicated the data were subjected to an arcsin transformation in order to normalise the distributions of the values around the means. In all other cases no differences between angular and proportionate values in the results of the tests were encountered and consequently the data are presented in p.feed A' form which relates most directly to the actual happenings in the experiment.

P1: The simplest test of the proposition that the diet was selected in a directed manner is to test the overall grand mean of p.feed A' [635 (s.e. 70)g/kg TFI] against the expectation that p.feed A' = 500g/kg TFI, that is a choice made at random. However, a closer look at the data for treatments 1-3, presented in Fig. 2.7 indicated the folly of such a test; p.feed A' for treatment 1 (377 s.e. 94) lies below the hypothesis of randomness whilst p.feed A' for treatment 3 (844, s.e. 38) lies significantly ($p < 0.01$) above it. Therefore, the indication from the data was that diet selection had differed, in a systematic fashion, from the expectation of randomness.

P2: The inclusion of treatment 4 in this experiment admitted a formal test of proposition (P2). In this instance, however, it was not possible to estimate the degree of confidence in the expectation that p.feed A' was not 1000g/kg TFI since the p.feed A' value was not common to both treatments. Hence the expectation was rephrased to be that the lambs will avoid completely feed D', that is, p.feed D' = 0.

With untransformed data (Table 2.11), the expected outcome for treatment 4

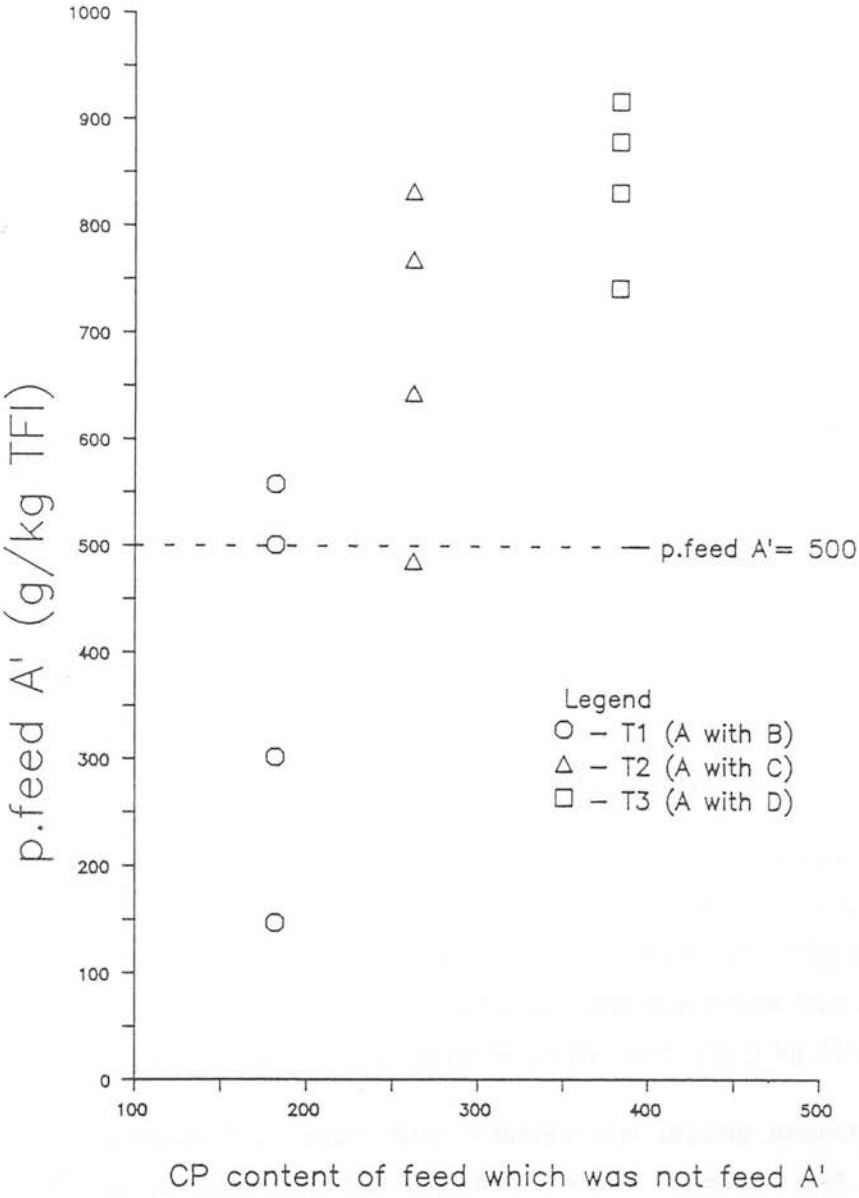


Fig. 2.7 The Effect of Treatment on the Composition of the Diet Selected by the Lambs

was not significantly different ($p > 0.1$) from that recorded. Furthermore, p.feed D' was found to be significantly smaller ($p < 0.05$) when the other feed was B' rather than A'. Additional tests using the transformed data were made in this instance due to the obvious skewness in the distribution of the p.feed D' values. Transformed p.feed D' was found to be significantly different ($p < 0.05$) from the expected outcome, indicating that the lambs were consuming some of feed D'. The difference between transformed p.feed D' for treatments 3 and 4 was not significant ($p > 0.1$). Thus, the transformed data gave a less dramatic picture of the avoidance of feed D' than the untransformed data. However, since the avoidance of feed D' was strongly evident, it was considered that the experimental resources of treatment 4 could be more effectively directed towards other parts of the experimental programme and so the treatment was ended after four weeks.

P3: The data presented in Fig. 2.7 have indicated that p.feed A' was dependent on the nature of the other feed on offer. Since each of these other feeds,that is, feed B', C' or D', included different proportions of feed A' when they were mixed, it was possible to calculate the proportion of the total feed intake as component feed A' (p.comp. A'). Table 2.12 shows the corresponding treatment means calculated from the data of individual lambs.

The p.comp A' data may be used to test the first expectation of proposition (P3) that all the lambs will select a diet of a certain composition, that is, p.comp A' is constant across treatments. Analysis of variance showed no significant treatment, period or sex effects ($p > 0.1$). Proposition (P3) therefore withstood the test of the data and it may be seen that the lambs had selected a common diet with an overall mean p.comp A' of 807 (s.e. 23) g/kg TFI.

The results obtained from Exp.1 have enabled the second expectation of proposition (P3) to be asserted, that the lambs would select a diet with an overall mean CP content of 147 (s.e. 3.3)g/kg TFI . On the basis that p.comp A' was similar between treatments over periods, and that the lambs were very close to 25kg LW at the beginning of the experiment, it was permissible to compare the observed mean CP content of the diet selected by the twelve lambs [149 (s.e. 6.8)g/kg TFI] in this experiment with that of the expected value. The two values were not significantly different ($p > 0.25$) from each other. However, the analysis of the p.comp A' data has already revealed that the composition of the diet selected did not change significantly within the ten

Table 2.12 The Effect of treatment on the Proportion of the Total Feed Intake (TFI) taken as component feed A' (p.comp.A', g/kg TFI)

p.comp.A' (*s.e.*)	Period 1	Period 2	Overall
Feed Pair			
T1 (A' with B')	800 (*30*)	789 (*35*)	788 (*29*)
T2 (A' with C')	784 (*68*)	791 (*45*)	789 (*51*)
T3 (A' with D')	864 (*21*)	837 (*46*)	844 (*38*)
Period mean	816 (*26*)	805 (*24*)	807 (*23*)

Table 2.13 The Change in the Composition of the Diet Selected (p.feed A', g/kg TFI) in Treatment 1

Lamb Identity	Period 1 (0-7 weeks)	Period 2 (7-14 weeks)	Period 3 (14-21 weeks)
1	465	630	784
2	597	559	724
3	341	428	794
Mean (s.e.)	468 (*74*)	539 (*59*)	767 (*22*)

weeks of the main experiment. On the basis of the ten-week data, the expectation that the CP content of the diet selected fell must be rejected.

Nevertheless, the extra eleven weeks of data available for treatment 1 allowed a test of the expectations to be made over a longer time-span. The data for the three surviving lambs of treatment 1, presented in Table 2.13, are divided into three arbitrary seven-week periods to facilitate a simple analysis.

It is apparent that there was a significant ($p < 0.05$) increase in p.feed A' between periods, which corresponds to a significant decrease in the CP content of the diet selected. The data of this experiment are compared with those of Exp.1 in Fig. 2.8. Furthermore, as a summary of the results of diet selection, figures which show the plot of cumulative differences in intake of feed B' and feed A' (Cum.diff.BA) have been used again to describe the essential character of the path of diet selection in lambs (see Fig. 2.9). For all three lambs, in accordance with the expectations, the path of diet selection showed a gradual transition from a diet of high CP content to one of low CP content.

C1: An analysis of the variance in daily rate of TFI indicated no significant differences between sexes or treatments ($p > 0.25$), which result was not different from that expected by corollary (C1). Secondly, the average daily rate of TFI for period I, at 1045g/day (s.e. 59) was not significantly different ($p > 0.1$) from the expected rate of 1248g/day. Furthermore, the analysis of variance indicated that daily rate of TFI increased in Period II ($p < 0.001$), again in accordance with expectations. Finally, the ten-week TFI of 101.2kg (s.e. 4.4) was not significantly different ($p > 0.1$) from the 102.1kg expectation, which was based on the data of Exp.1. However, a presentation of the data in graphical form (Fig. 2.10) indicated that the rate of TFI deviated systematically in Exp.2 from that which was recorded in Exp.1. Rate of TFI started off lower and ended higher in Exp.2.

C2: The expectation of corollary (C2) that the lambs on Treatment 5 would take feed at a similar rate to choice-fed lambs was tested by a t-test comparison of daily rate of TFI in the two periods. Treatment 5 lambs did not eat at a significantly different ($p > 0.1$) rate than choice-fed lambs.

C3: The TFI data of the lambs in Treatment 6 were subjected to an analysis of variance, as a test of the expectation that Treatment 6 lambs would have an initially higher rate of TFI. The rate of TFI for Treatment 6 in both periods, was

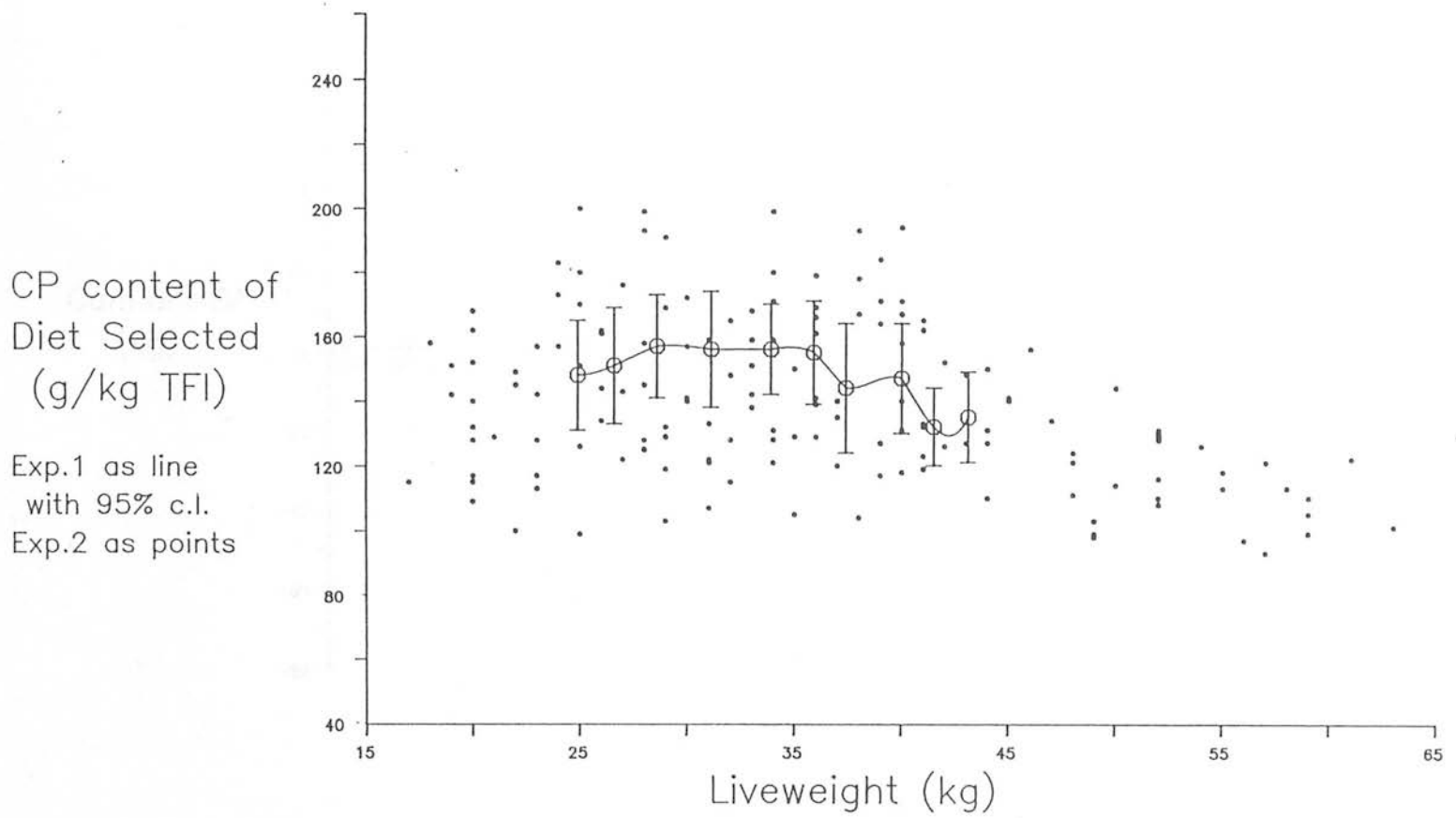


Fig. 2.8 The Crude Protein (CP) Content of the Diet Selected by Growing Lambs (Exp.1 and Exp.2 compared)

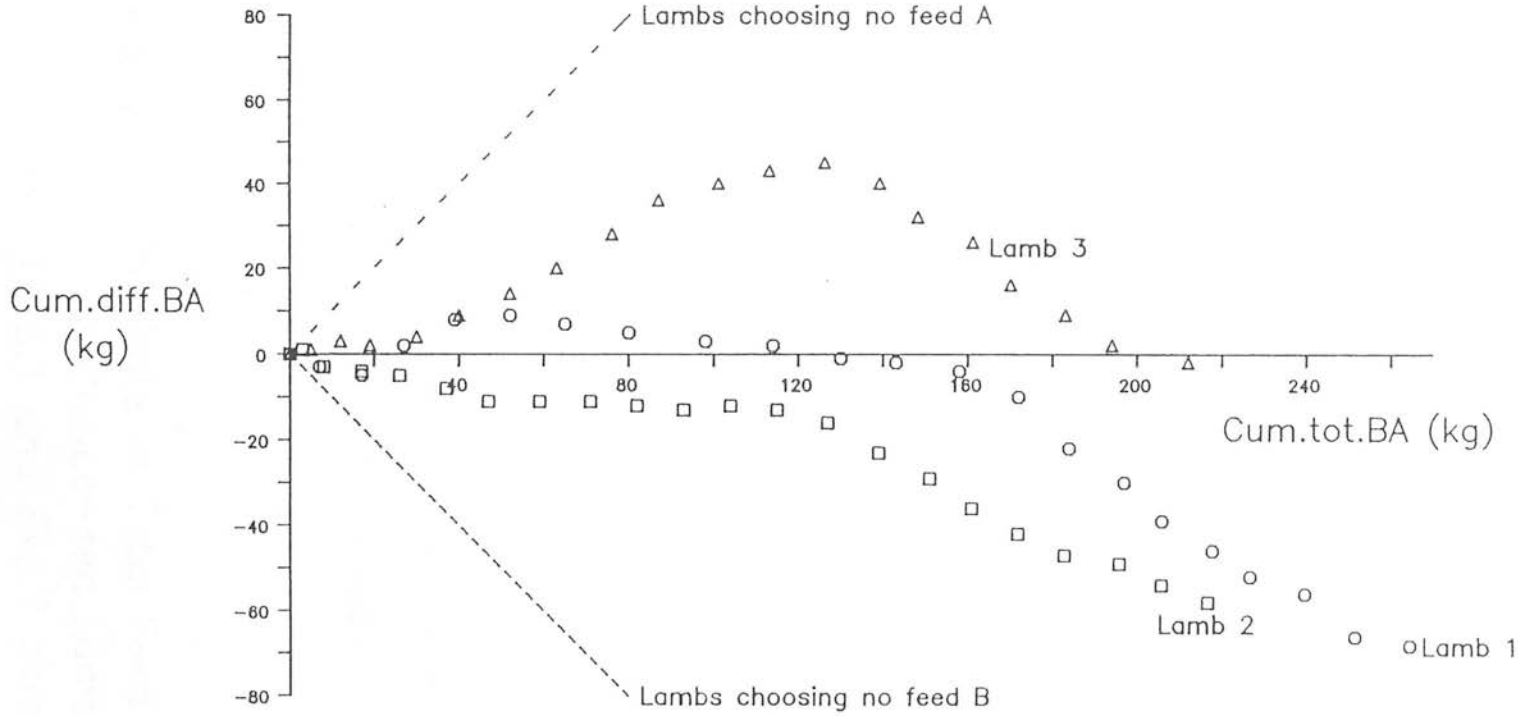


Fig. 2.9 Paths of Diet Selection in Growing Lambs

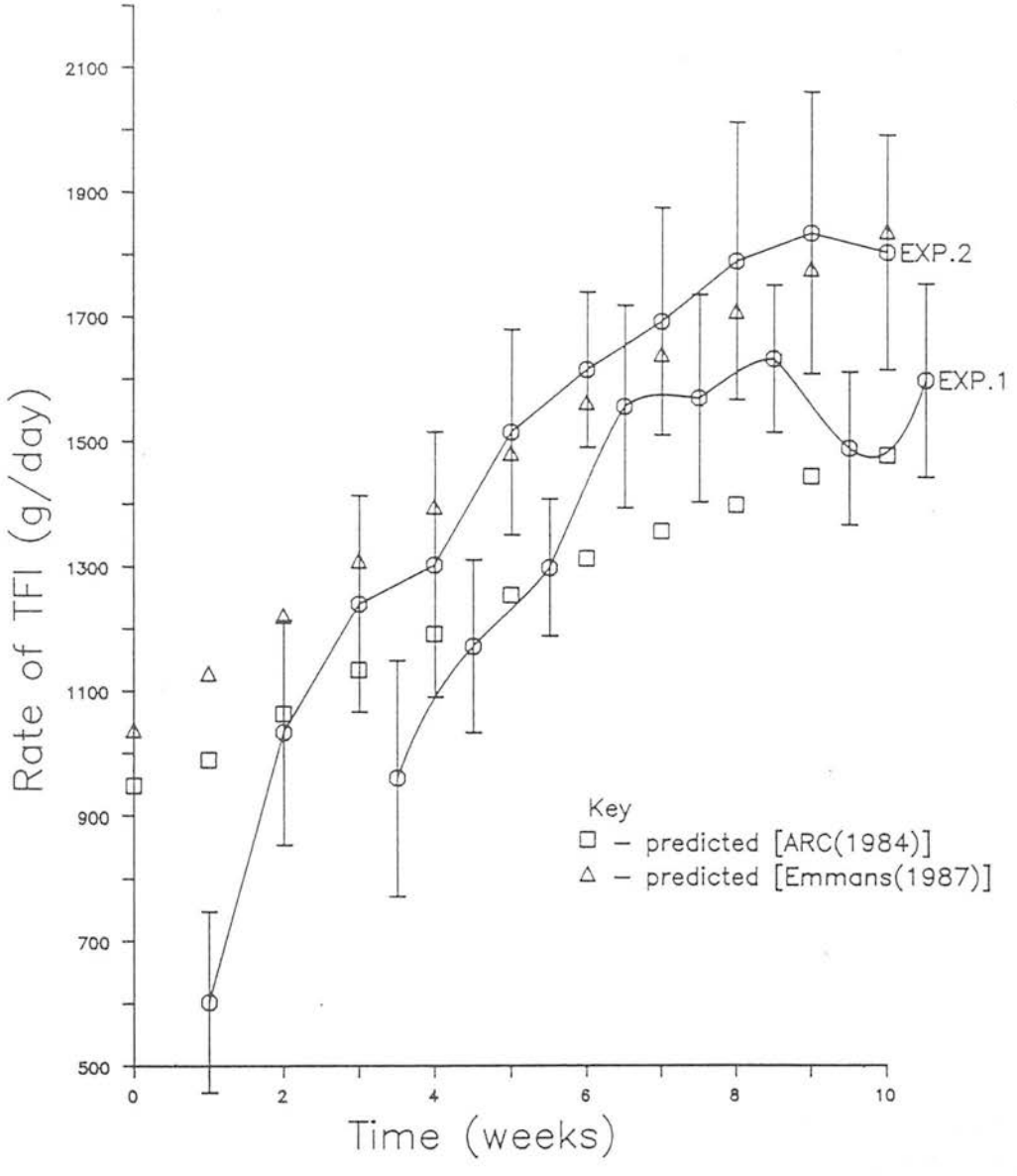


Fig. 2.10 The Rate of Total Feed Intake (TFI) of Choice–fed Lambs (Exp.1 and Exp.2 compared)

Table 2.14 The Effect of Treatment on the Estimate of the Gompertz Rate parameter (B) for Liveweight Gain

Treatment	n	Feed 1	Feed 2	B ($x10^{-3}$)	s.e. ($x10^{-3}$)
1	4	A	B	9.10	0.73
2	4	A	C	9.13	0.96
3	4	A	D	8.60	0.96
4	4	B	D	10.10	1.10
5	3	B	-	9.01	0.58
Total	19			9.20	0.38
6	4	A	-	8.17	0.52

found to be lower, but not significantly lower ($p > 0.1$) compared with all the other treatments, which was contrary to expectations.

C4: A Gompertz analysis of LWG using an estimated mature LW of 100kg yielded estimates of the rate parameter, B, for the six treatments, as given in Table 2.14. There were no significant ($p > 0.25$) differences between the four choice-fed treatment groups, in agreement with the expectations of corollary (C4). The average rate of LWG for these lambs was 319 (s.e. 18)g/day.

C5: As expected, there was no significant ($p > 0.25$) difference between the B value of the choice-fed lambs and those offered feed B' only. However, all of these lambs collectively had a B value of 0.0092 (s.e. 0.0004) which was significantly greater ($p < 0.05$) than the expected rate [0.0078, s.e. 0.0003] from Exp.1

C6: The lambs given feed A' only had an estimated B value for LWG of 0.0082 (s.e. 0.0005), which was in the expected direction but was not significantly different ($p > 0.1$) from that of the rest of the lambs.

2.7.5 Discussion

The recorded outcomes departed from the expectations in two main areas of the experiment.

(i) The lambs of treatment 4 chose a measurable proportion of the high CP content feed D' in their total feed intake when a total avoidance of that feed was expected. In absolute terms, however, the choice of the lambs on Treatment 4 was overwhelmingly away from feed D'. It was suggested in the review that animals may continue to test small quantities of, in this instance, an imbalanced feed in order to remain informed about any changes in the quality of the feeds on offer. After formal statistical analysis this minor effect may have come to be significant but such an outcome should not be taken as evidence against the idea that lambs seek to minimise excess protein intake.

(ii) At first glance the discrepancies in TFI and LWG between the choice-fed lambs of Exps. 1 and 2 may appear to undermine the proposed theory of diet selection. An attempt is now made to explain these anomalies which imply that the lambs in Exp.1 did not have, or were not able to express, the same

potential for growth as the lambs in Exp.2.

In both experiments the lambs used were of the Suffolk X Greyface type, but were obtained from different farms. Thus there remains the possibility that the sires, or dams, or both parents of the lambs in Exp.2 had a larger mature size than those in Exp.1, a factor which would explain at the outset the greater growth potential and the greater feed intake required to support the growth of the lambs in Exp.2. Consequently, in terms of the opportunity to express the potential for growth, it should be remembered that the digestibility and nutritive value of the pairs of feed on offer were similar, save for CP, and that the evidence of the diet selection provides good grounds for believing that the lambs, in both experiments, were regulating their total feed intake on the basis of their requirements for energy. The problem then arose of predicting the energy requirements of the lambs as feed equivalents.

Once again, the models of ARC (1984) and Emmans (1987,1988) were compared with the feed intake data. Emmans' model predicts the feed intake needed to satisfy the energy requirements for maintenance, growth and fattening. Therefore, the close agreement between the predicted and recorded rates of feed intake (Fig. 2.9) strengthened the argument that the lambs were not limited by nutrient intake.

The ARC model, however, which was an adequate predictor of feed intake in Exp. 1, was found to deviate greatly from the data in this experiment. The cause of this disagreement is not considered to be that the lambs failed to select a non-limiting diet, but to be a reflection of the rationale of the model itself. The ARC model predicts feed intake from a knowledge of only LW and q, the metabolisability of the feed. This procedure treats all sheep of a given LW as equals regardless of possible differences in degree of maturity and growth potential (e.g. between breeds of different mature size) and possible differences in composition of the gain.

Finally, the absence of the expected differences in growth and feed intake of lambs offered feed A' only is attributed to an experimental design that allocated too few lambs to the treatment to attain significance, and that began with lambs whose degree of maturity reduced the relative severity of the treatment. Consequently, had more lambs been taken at lower liveweights, it is still expected that the effect of a single feed of low nutrient: energy ratio

offered *ad libitum* would be to reduce growth rate and feed conversion efficiency.

The design of the experiment benefitted from the improvements suggested in Exp.1. The greater difference in the CP content of the feed on offer rendered the variation around the mean treatment values to be less influential on the statistical significance of the results than in Exp.1. The illustrative paths of diet selection (Fig. 2.9) produced curves of the same type as in Exp.1, showing a gradual transition from a diet of high CP content to one of low CP content.

Taking into account liveweight, the closeness between Exps.1 and 2 in the CP content of the diet selected, despite the two quite different ranges of choice offered, is most immediate in the plot of Fig. 2.8. Again, the values are in the range considered by NRC (1985) to be the requirement of similar lambs. However, this outcome is not hailed as 'proof' of a CP requirement in lambs, since there are reasons to doubt the usefulness of such a scale and to speculate on the influence on diet selection of an unmeasured nutrient other than CP or an amino acid. Nevertheless, allied to the finding that growth rate equalled or surpassed that previously recorded in the sheep type, choice-feeding has opened itself to the interpretation that it is a means of determining the animal's requirement for a given resource. Choice feeding has been demonstrated to be an alternative method to *ad libitum* feeding of single feeds for the provision of non-limiting conditions for growth. It is the charge of future researchers to decide how much further the implications of the approach can be taken in nutrition science.

2.7.6 Conclusions

The experimental evidence has offered substantial support to the propositions and corollaries which embody the theory that lambs are capable of expressing their complete inheritance when given the opportunity to select a balanced diet. It is therefore concluded that the lambs selected a diet

(a) in a directed manner.

(b) which minimised excess protein intake.

(c) which, at each successive degree of maturity, was not first limiting in a nutrient and hence, in quantity, reflected their energy requirements for maintenance, growth and fattening.

(d) which supported the full expression of their inheritance.

2.8 Experiment 3: A Test of the Rules for the Choice of Feed Bulkiness.

2.8.1 Objectives

The literature review betrayed the shortage of information (from controlled-environment experiments) which can be used to test the proposed, but largely unsubstantiated, 'rules' for the choice of feed bulkiness.[9] Such information is considered to be important for the prediction of feeding behaviour and growth of lambs reared under field conditions, in which the feeds on offer are frequently limiting to growth through the incapacity of the animals to eat enough of them. Therefore, the purpose of this experiment was to test several propositions concerning diet selection, feed intake and growth from lambs given free and continuous access to two feeds, of similar protein content but which differed in their digestibility.

2.8.2 Propositions

The simple notion that lambs, when offered two feeds of different bulkiness, will minimise their feeding time and intake of ballast was adopted as the basis for the propositions of this experiment. Consequently, it was expected that lambs, when offered two feeds of different bulkiness,:

P1: will select a diet in a directed manner.

P2: will completely avoid the more bulky feed of the pair.

2.8.2.1 Corollaries

Should all the lambs favour the less bulky (non-limiting) feed, their growth will not be first limited by a nutrient, in which case the following corollaries apply:

C1: all the choice-fed lambs will have a similar TFI which is dependent on,

[9] The term 'bulk' is used in this experiment to denote feeds of low digestibility and bulk density. In this case, the differences were achieved by incorporating processed straw into the feeds (see Materials and Methods.)

and predictable from, their energy requirements for maintenance, growth and fattening.

C2: lambs offered the less bulky feed alone will have similar TFI characteristics to choice-fed lambs.

C3. lambs offered more bulky feeds alone will eat, according to the bulkiness of that feed,

(a) more feed to reach DFI (energy).

(b) less feed and fail to reach DFI (energy) when limited by bulk.

C4: all choice-fed lambs will grow at the rate set by their inheritance i.e. they will have a Gompertz B rate parameter value which is not different from the expectation of 0.0092.

C5: lambs offered the less bulky feed alone will have similar B values for LWG to the choice-fed lambs.

C6: lambs offered more bulky feed alone will,

(a) have similar B values for LWG to choice-fed lambs.

(b) have lower B values for LWG than choice-fed lambs when bulk becomes limiting.

2.8.3 Materials and Methods

Animals 28 Suffolk X Greyface wethers (n = 14) and females (n = 14) at an age of approximately seven weeks and an average LW of 19.2 (s.d. 2.4)kg were purchased from the same commercial farm as in Exp. 2. Four extra lambs were also drafted into this experiment from treatment 4, Exp. 2, four weeks after the beginning of the experiment (see Design).

Feeds Four pelleted feeds were required which had an abundance of protein, minerals and vitamins but which differed in digestibility and bulk density. The dilution method for mixing these feeds, described in Exp. 1, was employed once again and the basal feed mixed first, without molasses.

The least bulky (non-limiting) basal feed was of the same formulation as feed B' in Exp. 2 and will continue to be labelled feed B'. It was planned to effect the difference in digestibility between the two basal feed by substituting ground wheat straw for the barley and sugar beet pulp in feed B'. However, as the feed milling facilities were not able to handle the quantities required for the experiment, nutritionally improved straw pellets [10] were taken instead and crushed for the purposes of mixing. All of the barley and sugar beet pulp, and 0.018 of the fishmeal in feed B' were replaced by 0.759 of the treated straw to form feed Z (see Table 2.15).

The range of four feeds of different digestibility was made from mixtures of feeds B' and Z. Feed X was a mixture of 2/3 B' and 1/3 Z. Feed Y was made from 1/3 B' and 2/3 Z. A proximate analysis of the feeds was carried out and the results are given in Table 2.16.

Experimental Design The 28 lambs were balanced for sex and randomly allocated to one of seven treatments. The main experimental treatments lasted for eleven weeks. Treatment 8, however, began at week 4 and will be treated separately from the rest. The design of the experiment is given in Table 2.17.

Management The housing and penning facilities were identical to those described in Exp. 1 and Exp. 2. The weighing and feeding routine was also the same as in Exp. 2; the two experiments were run at the same time.

2.8.4 Results

The eleven weeks of the experiment have been divided into two periods (Period I, weeks 1-4; Period II, weeks 4-11) in order to include the data of Treatment 8 and make comparisons with Exp 2. The actual weekly feed intake and liveweight data of individual lambs can be found in Appendix D. There were four deaths in the experiment: lambs 18 and 19 (Treatment 3), lamb 45 (Treatment 5) and lamb 40 (treatment 7). Their data have been completely excluded from the analysis. Lamb 18 was replaced by lamb 13 in week 4 when Treatment 6 began.

[10] VITON-NIS (NaOH treated straw) from Unitrition International Ltd: Analysis (%), Oil (1), crude protein (4.2), U.D.P. (1.0), crude fibre (36), Digestible fibre (25), Ash (10.5), Metabolisable energy (9.1MI/kg DM), Sodium bicarbonate equivalent (3).

Table 2.15 The Composition of the Basal Feeds (g/kg freshweight) in Experiment 3

Ingredient	Feed B'	Feed Z
Ground barley	313	0
Sugar beet pulp	440	0
White fishmeal	190	172
Viton NaOH straw	0	759
Urea	0	19
Dicalcium phosphate	3.8	0
Ground limestone	2.2	0
Salt	1.5	0
Nutrikem sheep trace element/vitamin mix	2.5	2.0
Molasses	47.0	48.0
	1000.0	1000.0

Table 2.16 The Chemical Analysis of the Feeds (g/kg freshweight) in Experiment 3

	Feed			
Constituent	B'	X ($\frac{2}{3}$B'+$\frac{1}{3}$Z)	Y ($\frac{1}{3}$B'+$\frac{2}{3}$Z)	Z
Crude protein	182	184	180	167
Ether extract	23	24	22	20
Ash	96	100	102	104
Dry matter	878	882	881	914
Crude fibre	79	141	211	283
MAD fibre	76	186	269	362
Digestibility of organic matter	0.90	0.83	0.77	0.70
Metabolisable energy[a] (MJ/kg)	12.2	10.6	9.9	9.3
Bulk density (kg/m^3)	687	487	415	342

[a] values calculated from feed tables

Table 2.17 The Design of Experiment 3

Each lamb was offered continuous *ad libitum* access to one or two feeds:

Treatment	n	Feed 1	Feed 2	Duration (weeks)
1	4	B	Z	11
2	4	B	Y	11
3	4	B	X	11
4	4	B	-	11
5	4	X	-	11
6	4	Y	-	11
7	4	Z	-	11
8	3	X	Z	7

Table 2.18 The Effect of Treatment on the Composition of the Diet Selected (p.feed 1, g/kg TFI)

Treatment	n	Feed 1	Feed 2	p.feed 1	(*s.e.*)	Significance of difference from random choice†
1	4	B	Z	649	(*40*)	**
2	4	B	Y	684	(*62*)	**
3	3	B	X	494	(*32*)	n.s.
Total	11			619	(*35*)	***
8	3	X	Z	962	(*26*)	***

† ***, $p<0.001$; **, $p<0.01$; *, $p<0.05$; n.s., $p>0.1$

A similar analysis to that made in Exp. 1 and Exp. 2 was adopted for this experiment: the proportion of the TFI which was taken from the trough which contained feed B' became p.feed B', a measure common to Treatments 1-3.

P1: The mean p.feed B' value of 619 (s.e. 35)g/kg TFI (Table 2.18) for treatments 1-3 differed significantly ($p < 0.001$) from the expectation that p.feed B' = 500g/kg TFI. This outcome agreed with the expectation of proposition (P1) that lambs would choose a diet in a directed manner.

P2: However, the same mean indicated that diet selection was significantly different ($p < 0.001$) from the expectation of proposition (P2) that p.feed B' = 1000g.kg TFI.

This outcome prompted a closer look at the diet selection in each treatment (see Table 2.18). The diet selected by lambs on Treatment 1 [p.feed B' = 649 (s.e. 40)g/kg TFI] and Treatment 2 [684 (s.e. 62)g/kg TFI] were found to differ significantly ($p < 0.01$) from the expectation of randomness. For Treatment 3 [p.feed B' = 494 (s.e. 32)g/kg TFI], it was not ($p > 0.1$). Nevertheless, when the choice was offered between feeds X and Z (Treatment 8), the lambs showed a significant avoidance ($p < 0.001$) of the more bulky feed Z (p.feed Z = 38 (s.e. 26)g/kg TFI), an outcome which did not differ from expectations. Furthermore, p.feed X differed significantly ($p < 0.01$) when the other feed was Z (962 s.e. 26) that when it was feed B' (506 s.e. 32). The value for p.feed Z differed significantly ($p < 0.01$) when the other feed was X (38 s.e. 26) than when it was feed B' (351 s.e. 40).

C1: The average rate of total feed intake of the choice-fed lambs (Treatment 1-3) was 1213 (s.e. 74)g/day in the first four weeks rising to 1829 (s.e. 49)g/day in weeks 4-11. As was expected, there were no significant ($p > 0.1$) treatment differences.

C2: At no point in the experiment did the rate of total feed intake differ significantly ($p > 0.1$) for the choice-fed lambs (though it tended to be greater in both periods) from that of lambs offered feed B' only (see Fig. 2.11). This outcome was in agreement with the expectations.

C3: The relationship between rate of total feed intake and the proportion of component feed Z in the single feed on offer in Treatments 4-7 in period I , is presented graphically in Fig. 2.12. The prediction that lambs would increase

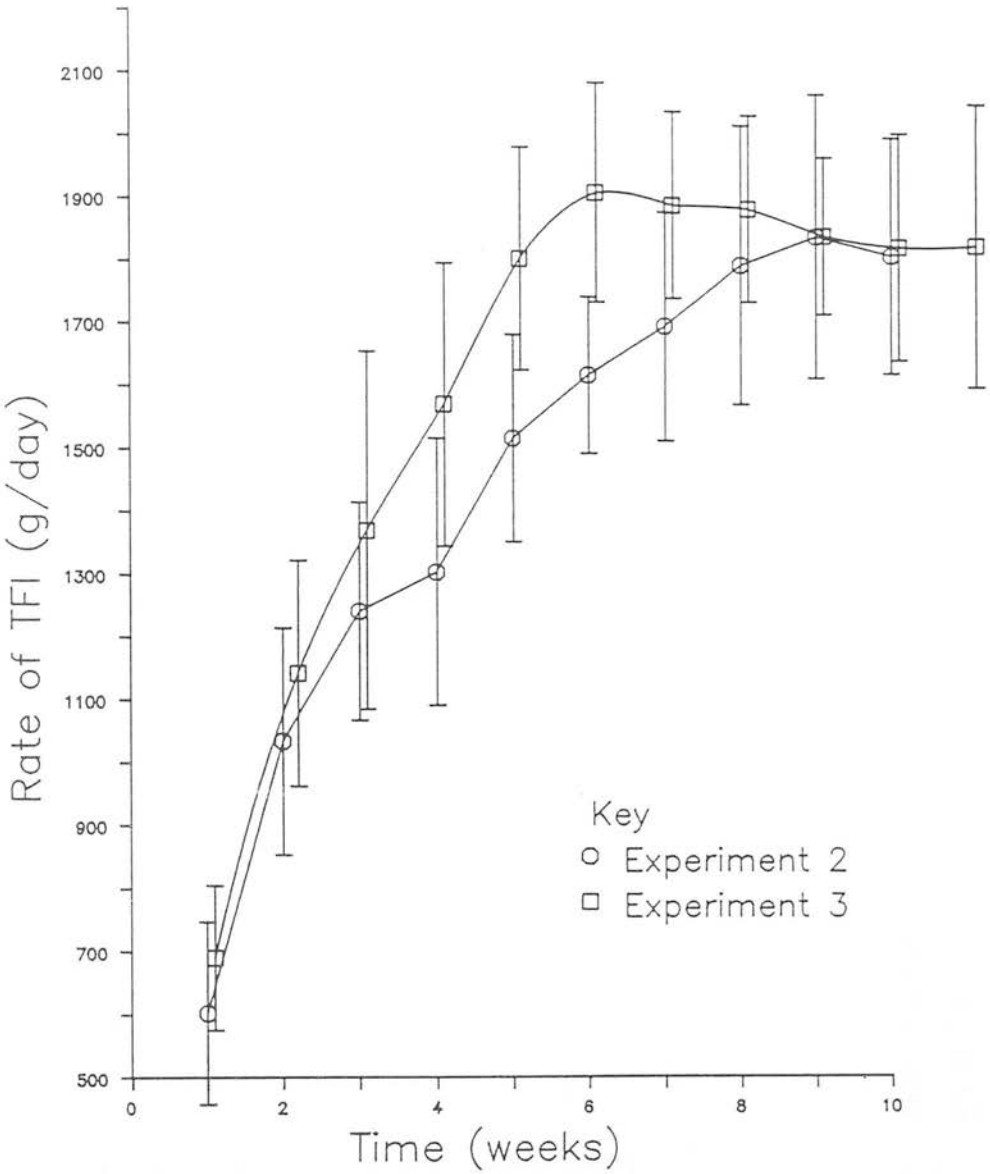


Fig. 2.11 The Rate of Total Feed Intake (TFI) of Choice-fed Lambs (Exp.3 and Exp.2 compared)

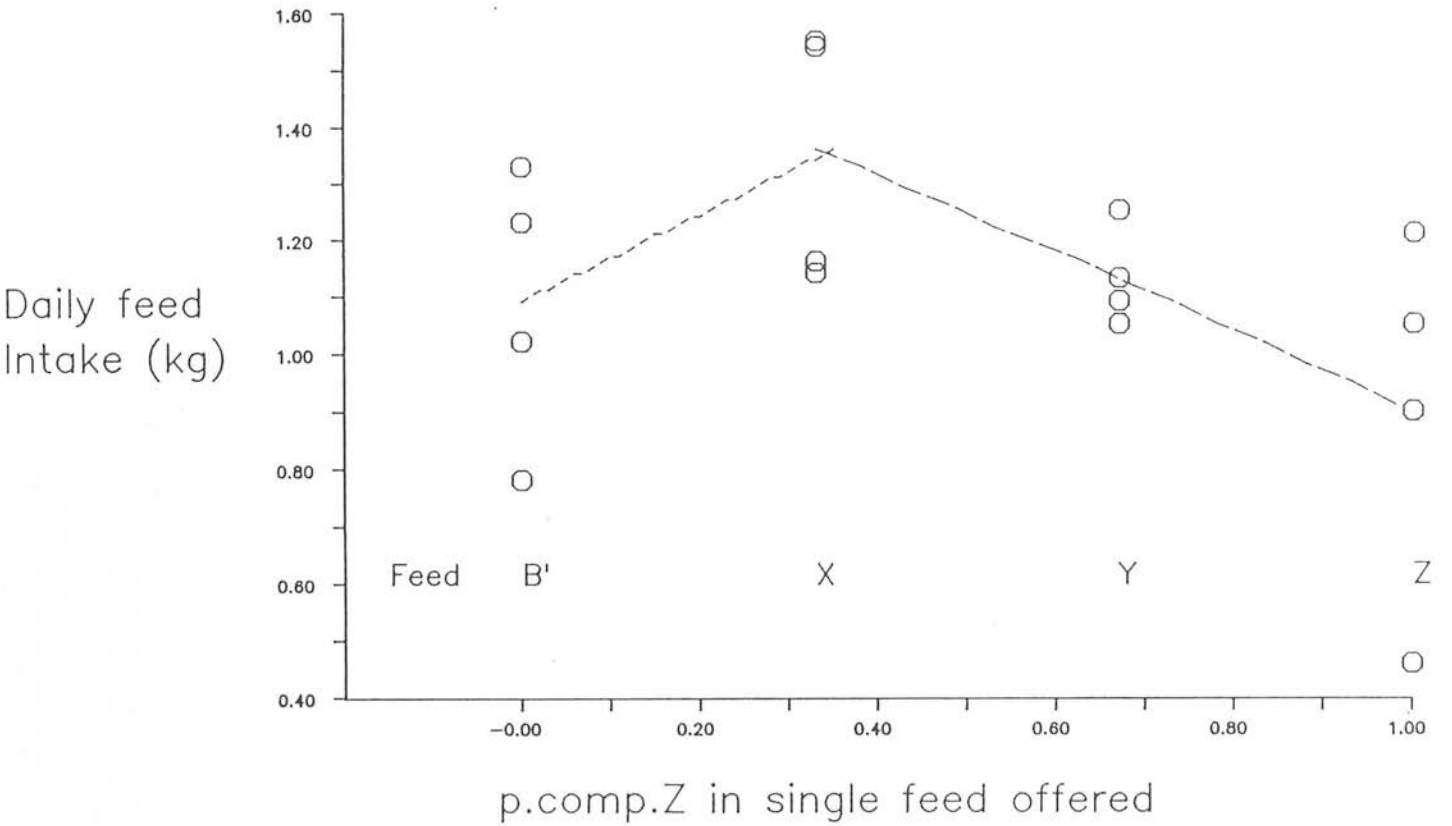


Fig. 2.12 The Relationship between Rate of Feed Intake and the Proportion of Component Feed Z (p.comp.Z) in the Single Feeds Offered

Table 2.19 The Effect of Treatment on the Estimate of the Gompertz Rate parameter (B) for Liveweight Gain

Treatment	n	Feed 1	Feed 2	B ($x10^{-3}$)	s.e. ($x10^{-3}$)
1	4	B'	Z	9.87	0.77
2	4	B'	Y	9.18	0.36
3	3	B'	X	8.48	0.60
4	3	B'	-	8.54	0.41
5	4	X	-	9.51	0.76
6	4	Y	-	8.01	0.88
7	3	Z	-	7.13	0.39
8	3	X	Z	9.17	0.72

their feed intake on the bulkier feed X but decrease their feed intake as bulk became limiting (feeds Y and Z) was qualitatively supported by these data. A model of the type suggested by Conrad *et al* (1964) and Dinius and Baumgardt (1970) has been fitted by two separate regressions (see Fig. 2.12) but the small number and high variability of the data did not permit an accurate estimate of the feed composition which represented a constraint on feed intake through bulk. From the graph it can be taken as a feed containing 0.33 feed Z. Furthermore, this constraint on intake was passing since in weeks 4-11 there were no significant differences ($p > 0.1$) between any of the eight treatments in their rate of total feed intake.

C4: A Gompertz analysis of LWG, using an estimated mature LW of 100kg, yielded estimates of the rate parameter, B, for the eight treatments, as given in Table 2.19. There were no significant differences ($p > 0.1$) between the four choice-fed treatments and the combined value of 0.0092 (s.e. 0.0003) was not significantly different from the expected value of 0.0092. The average rate of LWG of the lambs was 338 (s.e. 16)g/day.

C5: Lambs offered feed B' alone did not differ significantly ($p > 0.1$) in their B value (0.0085, s.e. 0.0004) from choice-fed lambs, in agreement with expectations.

C6: Lambs offered feed X alone also did not differ significantly ($p > 0.1$) in their B value (0.0095, s.e. 0.0008) from treatment 4 lambs or the choice-fed lambs. Lambs offered feed Y only and feed Z only did have lower B values, but only treatment 7 (feed Z) was significantly lower ($p < 0.01$). Treatment 7 lambs gained LW at an average rate of 251 (s.e. 12)g/day.

2.8.5 Discussion

The shortage of data concerning the diet selection of sheep given pairs of feeds which differed only in their bulkiness had encouraged the deliberate policy of testing a series of naive (some 'null') hypotheses in this experiment. The falsity of such a simple view was exposed immediately by the failure of the 'bulk-avoidance' theory to predict the diet selection and hence TFI and LWG of these lambs. Therefore, it is necessary to discuss further these results using the additional information from the single feed treatments to interpret the choices made. Since this experiment shares the information from Treatment 4

with that of treatment 5 Exp. 2, comments of LWG and FI from that experiment should be borne in mind during the discussion.

It was concluded in the previous experiment that feed B' was not limiting to growth. On the LWG criterion, feeds X and Y were not found to be limiting though feed intake on feed Y was depressed and it is possible that higher gut-fill weights in this treatment contributed to the apparently non-limited rate of LWG. Feed Z was certainly limiting and since FI was depressed, it may be concluded that it was limiting through its bulkiness.

Consequently, the set of choices offered did not give as wide a range as had been intended due to a limit on animal numbers and the unavoidable compromises in the feed formulation. In the context of the schema of section 2.5, the choices offered were:

Treatment	Feed 1 (less bulky)	Feed 2 (bulky)
1	B (*non-limiting*)	Z (*limiting*)
2	B (*non-limiting*)	Y (*marginally limiting*)
3	B (*non-limiting*)	X (*non-limiting*)
8	X (*non-limiting*)	Z (*limiting*)

The most striking result of the experiment was the refutation, at least in part, of the theory of optimal foraging (Krebs and McCleery, 1984) which had fostered the proposition that the lambs would minimise their bulk intake and feeding time. In treatments 1-3 there had been a significant intake of the more bulky feed. It could be argued that the ruminants which always take a small amount of roughage material would maintain their rumen microflora in a state of adaptiveness, such that they would be better able to digest new, fibrous feeds, should conditions change, than individuals eating only highly digestible feeds. However, since there was no apparent fixity between treatments of what could be termed a 'roughage requirement', this speculative theory cannot be substantiated and each treatment must be considered on its own.

Hence, given the nature of the choices on offer and the fact that lambs did not completely avoid the bulkier feeds, it became apparent that there was no

reason for the lambs in treatment 3 to favour either feed and that only treatments 1, 2 and 8 would they be expected to show a significant avoidance of the bulky feed. The tendency for choice-fed lambs to eat and to gain LW at faster rates than lambs offered feed B' only is attributed to the greater voluntary intake of bulk (see Fig. 2.11) in these treatments which, it is assumed, had a consequential effect on gut-fill weight and hence LWG. A more realistic comparison may be made between choice-fed lambs and lambs offered feed X only, where no differences were found. Dietary choice became more critical when the less bulky feed occupied more of the animal's capacity for bulk (treatment 8) such that only then did the animals minimise their intake of bulk. It is therefore possible that optimal foraging theory applies to only one case of the choices for feed bulkiness. It is suggested that the theory has been tested primarily under conditions where animals were given *non-limiting/ limiting* or *limiting/ limiting* choices, that is, under wild and agricultural field conditions where non-limited growth would never have been possible. The Rules of Diet Selection are offered once again as a perspective and guide to the interpretation of such studies. It would be the aim of future research to repeat the experiment using treatments with greater differences between the feeds in their bulkiness, as was originally intended. It would also be sensible to formulate the feeds in accordance with the methods of others (e.g. Dinius and Baumgardt, 1970) who have supplied information on the intake characteristics of single feeds. Of particular interest would be the testing of the *limiting/ limiting* option, which, it is believed, has immediate application to the prediction of grazing behaviour and feed utilisation of animals in the field.

2.8.6 Conclusions

This first experiment to test the Rules of Diet Selection for Feed Bulkiness permitted the following conclusions to be drawn.

1) Lambs, offered a choice between two feeds of high and non-limiting nutrient: energy ratio, but of different bulkiness, select a non-limiting diet.

a) by eating at random between the feeds when neither is limiting to growth.

b) by avoiding (but not completely) the bulk-limiting feed when such a strategy does not constrain desired feed intake.

c) by choosing exclusively the less bulky feed when desired feed intake would be constrained by any intake of the bulkier feed.

d) which is dependent on and predictable from their energy requirements for maintenance, growth and fattening.

e) which supports their potential for growth.

CHAPTER 3
THE GROWTH OF SHEEP UNDER LIMITING CONDITIONS.

3.1 Introduction - Three Possible Paths to Maturity

In Chapters I and II methods of describing the path of growth as determined by heredity, and the conditions which permit the attainment of the potential were proposed. The problem of predicting the growth of sheep under limiting conditions (that is, when one of the four conditions for non-limiting growth is not met) is now considered.

In his seminal paper entitled 'The Capacity of Animals to Grow under Adverse Conditions', Waters reported his observations on the growth of two groups of steers, which started the experiment close to their desired state, fed either (i) to maintain their bodyweight or (ii) to grow at the rate set by their potential.

The finding that

> for a considerable time after the animal was put on maintenance it increased in height quite as rapidly as did the animal which was fed to the limit of its appetite [and that] an ungrown animal may remain at constant body weight for a long period of time and yet increase in height and decrease in its stored fat

suggested to Waters that animals had more than one way (i.e. other than that described by the potential growth curve) of reaching maturity. He concluded that

> Apparently the animal has recourse to any or all of the following ways to reach a normal size.
>
> First, by growing steadily from birth to maturity, as with a uniform and ample food supply.
>
> Second, by storing fat in a period of abundant food supply to assist in tiding over a limited period of sparse food supply without serious interruption of growth.
>
> Third, by prolonging somewhat the growth period [since] an animal when sparsely fed through the early part of its life may grow after the time when an animal that was normally nourished is matured and has ceased to grow.
>
> Waters (1908)

To Waters, therefore, the way an animal reached its inherited mature size was subservient to the desire to achieve it, since animals have evolved ways of growing which allows them to attain the mature form for their species despite fluctuations in the feed supply.

The purpose of this review is to organise the ideas and experimental evidence on the subject of growth under limiting conditions, with particular reference to feed restriction (Waters' second and third 'path' to maturity). The responses of the animal in terms of the fat-free body will be considered first. Then, the important relationship between the nature of the feed restriction and the relative rates of growth and fattening will be presented.

3.2 A Theory of Growth under Restricted Feeding Conditions

3.2.1 The Diminution of the Gut Contents

ARC (1984) confirmed that the apparent digestibility of feed for ruminants increases as level of feeding is decreased from *ad libitum*. Given this knowledge, it must follow that the weight of faeces collected from a sheep under a feed restriction will be lower than that from a sheep fed *ad libitum* of the same feed. However, ARC (1984) also report that 'plane of nutrition has a surprisingly small effect on the gut-fill of ruminants' which would appear to indicate that an argument based on digestibility of the feed cannot be simply extended to predicting the weight of gut contents, composed of partially digested feed and water, as well as faeces. Nevertheless, a long interval between the last feed or water intake and the recording of gut-fill would presumably result in a decrease in the gut-fill of a restricted animal because of the smaller contribution of water or partially digested feed to the total weight of gut-fill. Consequently, there are data to support the idea that restricted sheep decrease their weight of gut-fill (Mitchell, Kammlade and Hamilton, 1928; Burton, Anderson and Reid, 1974; Murray and Slezaceck, 1976)

3.2.2 The Fixity of Form in the Lipid-free Empty Body

Hammond (1932) initiated a series of experiments on the effect of a feed restriction on the growth and tissue yields of pigs (McMeekan, 1940), lambs (Palsson and Verges, 1952), poultry (Wilson, 1952, 1954) and goats (Wilson, 1958). The conclusions drawn from this work became widely accepted, and are typified by the words of Palsson (1955).

> (a) During late foetal life to maturity, any part, organ or tissue of the animal's body is proportionately retarded in development by restricted nutrition at the age when it has the highest natural growth intensity.
>
> (b) Restricted nutrition during any age interval, from late foetal growth until growth ceases, has an increasing retarding effect on the different tissues and parts of the animals body in the direct order of their maturity.

Such a conclusion came as a consequence of the way Palsson had chosen to analyse the data from his experiments. His inclination, evidently shared by the

Cambridge School, had been to compare between the treatments absolute and relative growth rate of each component and proportionate compositions at certain live- or carcase weights. This mode of analysis confirmed Palsson's view that each component of an animal responds independently and differentially, albeit in some kind of order, to a feed restriction.

However, an important feature of the work of Waters, which was confirmed later in the studies of Moulton *et al* (1922) and upheld by Murray (1919) was that, except in the most severe cases of undernutrition, the different ways of reaching maturity did not alter the proportions of the lipid-free empty body of animals during growth or at maturity. In Thompson's (1917) words:

> the form finally attained is so definite, and is little dependent on the time taken to effect it, that the specific rate of change, or rate of growth, does not enter into the morphological problem.

Therefore, it may be more helpful to say that the animal inherits a growth-plan which leads to a strongly fixed form for the lipid-free empty body at maturity. Independently of the rate at which maturity is attained, the animal has, at any particular degree of maturity during the expression of growth, a certain, largely invariant, form to the lipid-free body which successively keeps the animal in a state of fitness throughout the process of maturation. [11]

Consequently, this picture of animal development promotes the idea that an animal may respond to a feed restriction as a viable whole and contrasts with the view of the Cambridge school which emphasised the 'profound influence of nutrition on the animal body' (McMeekan, 1940) by measuring the differential growth of each component.

3.2.3 The Contraction of the Feed-processing Organs

The data of Moulton *et al* (1922) on the cattle of Waters (1908) were obtained to reassess the effect of a feed restriction on body form by the method of allometric analysis recommended in Chap. I for the description of the potential for growth in animals. The availability of chemical data for each

[11] The exclusion of fat from the issue is widely agreed upon (Elsley et al, 1964) in accordance with Waters' early proposition that fat is mobilised in the body when the animal is growing under adverse conditions.

anatomical component of the body improved the accuracy of the analysis since it avoided the problem of unequal lipid content in organs from well- and poorly-fed individuals. The results of the analysis confirmed the conclusion of Moulton *et al* (1922) that no differences between the two treatments in the relative growth of any of the components of the lipid-free empty body were present.

A similar reanalysis on the published data of Mitchell *et al* (1928) for growing sheep revealed again the expected fixity of form in the lipid-free empty body between lambs given fixed allowances of alfalfa and corn (0.7kg/day) and those offered the feeds *ad libitum*. However, the chemical data for the composition of the offal (head + skin + feet + viscera) showed a smaller contribution to total body protein (excluding wool) from the offal component in the poorly fed lambs at the same degree of maturity.

The greater part of the treatment differences reported for the anatomical components in the paper of Palsson and Verges (1952) vanished under the scrutiny of the same allometric analysis, as indicated by Elsley *et al* (1964). There was a fixed relationship, independent of feeding level, between carcase muscle and all the skeletal components (except the head) and the organs of respiratory system. However, the analysis showed that the sheep on the lower plane of nutrition had relatively less weight of stomach and less weight of liver than the lambs on the high plane.

Departures from the directives of the growth-plan in the visceral component of the sheep of Mitchell *et al* (1928) and Palsson and Verges (1952) may therefore be ascribed to the animal's truly adaptive ability to abate the growth of feed processing organs at a time when feed is scarce. The relationship between rate of feed intake and gutsize was introduced in Chap. I.

3.2.4 The Inconsistency of Wool Gain

The historical prominence of wool in agriculture encouraged the earliest sheep scientists to investigate the effects of nutrition on wool yield. Indeed, Kellner (1915), backed by reliable data, confirmed the common experience that wool growth slows down under conditions of poor feeding. Kellner and others (Fraser, 1935; Marston, 1935) were also prompt to recognise the major role that

wool has in the nitrogen economy of the sheep, particularly its requirement for sulphur-containing amino acids (Marston, 1935). Moreover, later research has shown that immature sheep under limiting conditions decrease their rate of wool growth to a lesser degree than their growth of body protein (Kellaway, 1973). The form of the lamb in terms of its wool: protein ratio may therefore depart from the directives of the growth-plan in response to poor feeding [12] However, since data from other studies (e.g. Mitchell *et al*, 1928) have already indicated that the wool: protein ratio does not deviate from normality in all restricted feeding situations, this proposition cannot be taken as universal. Consequently, the problems of relating yield and quality of wool to nutritional factors, particularly sulphur supply, are long-standing (see review by Ryder and Stephenson, 1968) and knowledge of the wool growth patterns of mature sheep, often taken as a standard, may not be applicable to the case of lambs growing under limiting conditions prior to their first moult.

[12] Analogous cases can be found in the abnormal growth of feathers in chickens and hair in pigs under severely restricted feeding conditions.

3.3 The Partitioning of Scarce Resources

A way of relating the desire of an animal to reach maturity to its need for certain feed resources (to satisfy that desire) was introduced in Chap. II, in the words of Waters (1908) as a feed requirement for '(a) Maintenance (b) Production of Growth [protein + water + ash] and (c) Production of Fat [lipid]'. In his scheme, growth of protein and ash were distinguished from fattening, and the former were seen as having priority for the resources during the growth period. Fat, or lipid, was identified as the variable component of the empty body, and was therefore regarded as a reserve of energy, given lowest priority during the growth period, which was mobilised as a source of supplementary energy whenever the energy yield of the feed was limiting to maintenance and growth.

Waters' proposals of the animal's rules for the partitioning of scarce resources form the basis of a workable theory which benefits from the addition of the qualification, asserted by Emmans and Fisher (1986) but acknowledged by Elsley *et al* (1964) and Black (1974), that the allowance of feed is better described in terms of its first limiting resource to growth. The resource will be either the first limiting nutrient or energy.

This helpful distinction has not been widely employed in the published literature. In the papers of Palsson and Verges (1952), Morgan and Owen (1972), McManus, Reid, and Donaldson (1972) and Thornton, Hood, Jones, and Re (1979) only the feed constituents are named. In the works of, for instance, Meyer and Clawson (1964), Andrews and Orskov (1970), Drew and Reid (1975), Murray and Slezaceck (1976) and Winter, Tulloh and Murray (1976) the quality of the feed is represented in terms of its derived crude protein and ash contents, which are more helpful but still limited descriptions of the nature of the restriction. Meanwhile, the genuine difficulties in predicting the yield of nutrients and energy of feeds for ruminants still confront the animal scientist.

Nevertheless, as an aid to understanding the response of an animal to any feed restriction, idealised predictions may be generated from a theory derived from Waters' rules for resource partitioning and the description of the allowance's first limiting resource.

3.3.1 A Model to Predict Protein and Lipid Gain under Restricted Feeding Conditions.

The five assumptions of the model are:

1) that the lamb puts a priority on its growth of protein.

2) that the lamb is capable of mobilising lipid in periods of energy shortage.

3) that the two feed variables of consequence are the ratio of the first limiting nutrient: energy and the rate of supply of the feed.

4) that the nutrient: energy ratio of a feed is independent of feed allowance.[13]

5) that the lamb may always be thermally neutral.

3.3.1.1 Allowances of a Balanced Feed

Suppose that a lamb is given a feed A which is balanced in terms of its first limiting nutrient and ME content. By the definition given in Chap. II, *ad libitum* intake of feed A (Fl_{al}) allows the lamb to grow at its potential rate (p^*) and lay down lipid at its desired rate (l^*) whilst remaining thermally neutral (Fig. 3.1).

i) When an allowance of feed A, less than *ad libitum*, is offered to the lamb

a) nutrient supply will fall below the requirement for p^* and protein growth will be reduced according to the efficiency with which the nutrient supply is used.

b) energy supply will fall below the requirement for l^*. Lipid gain will be dependent on the amount of energy available to the lamb after the expenditure of energy in the storage and synthesis of the limited protein gain. Rate of lipid gain will be a function of the energy cost of lipid storage and synthesis.

---

[13] In Chap. II, reasons for dismissing, at the outset, such an assumption for ruminants, particularly in relation to protein supply, were considered. However, this model persists in the attempt to draw a distinction between concepts which apply to animals (e.g. partitioning rules) and those which apply to feeds (e.g. nutrient: energy ratio) with the aim of determining whether manipulation of body composition in sheep is possible, in theory, before seeking ways of achieving it.

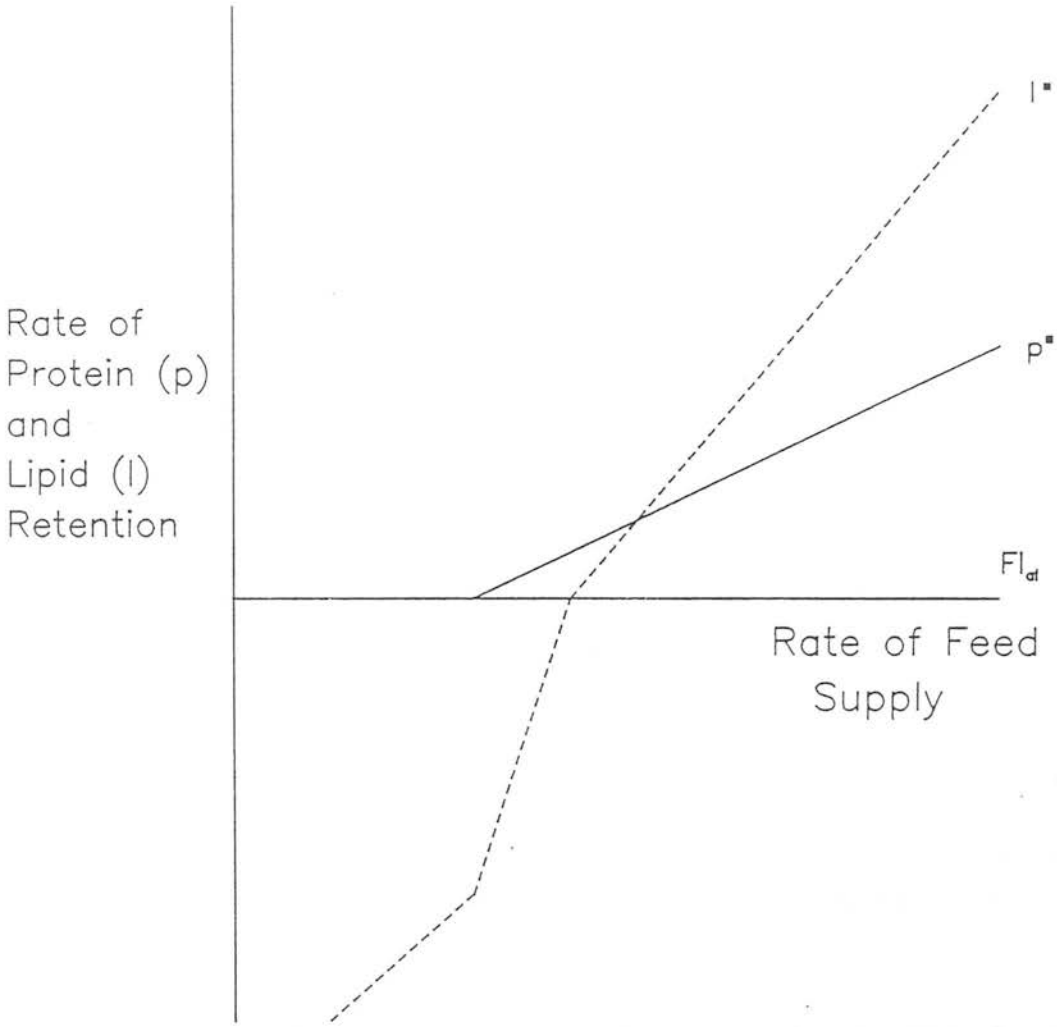


Fig. 3.1 Predicted Protein and Lipid Retention on Allowances of a Balanced Feed

2) When an allowance of feed A no longer supports lipid gain

a) nutrient supply may still permit a limited protein gain

b) lipid gain will be dependent on the amount of energy required to supplement the expenditure of energy in the storage and synthesis of the protein gain. Rate of lipid gain will be a function of energy supplied from mobilised lipid.

3) When an allowance of feed A no longer supplies sufficient nutrient for protein gain, lipid gain will be dependent on the energy available to the lamb after the expenditure of the energy for maintenance less the energy derived from mobilised protein. Rate of lipid gain will be a function of the energy supplied from mobilised lipid.

3.3.1.2 Allowances of an Imbalanced (nutrient-poor) Feed

Suppose that the lamb is now given a feed B which has the same ME content as feed A but a much lower nutrient: energy ratio (Fig. 3.2). *Ad libitum* access to feed B will allow the lamb to grow at its potential rate (p^*) but, in order to acquire sufficient nutrient for growth, it must consume energy excess to its requirement for desired lipid gain (l^*). The lamb will therefore use the excess energy intake to synthesise and store surplus lipid.

1) When an allowance of feed B, less than *ad libitum*, is offered to the lamb

a) nutrient supply will fall below the requirement for p^* and protein growth will be reduced according to the efficiency with which the nutrient supply is used.

b) lipid gain will be dependent on the amount of energy available to the lamb after the expenditure of energy in the storage and synthesis of the limited protein gain. Rate of lipid gain will be a function of the energy cost of lipid storage and synthesis.

2) When an allowance of feed B no longer supplies sufficient nutrient for protein gain, lipid gain will be dependent on the energy available to the lamb after the expenditure of energy for maintenance less the energy derived from mobilised protein. Rate of lipid gain will be a function of the energy cost of

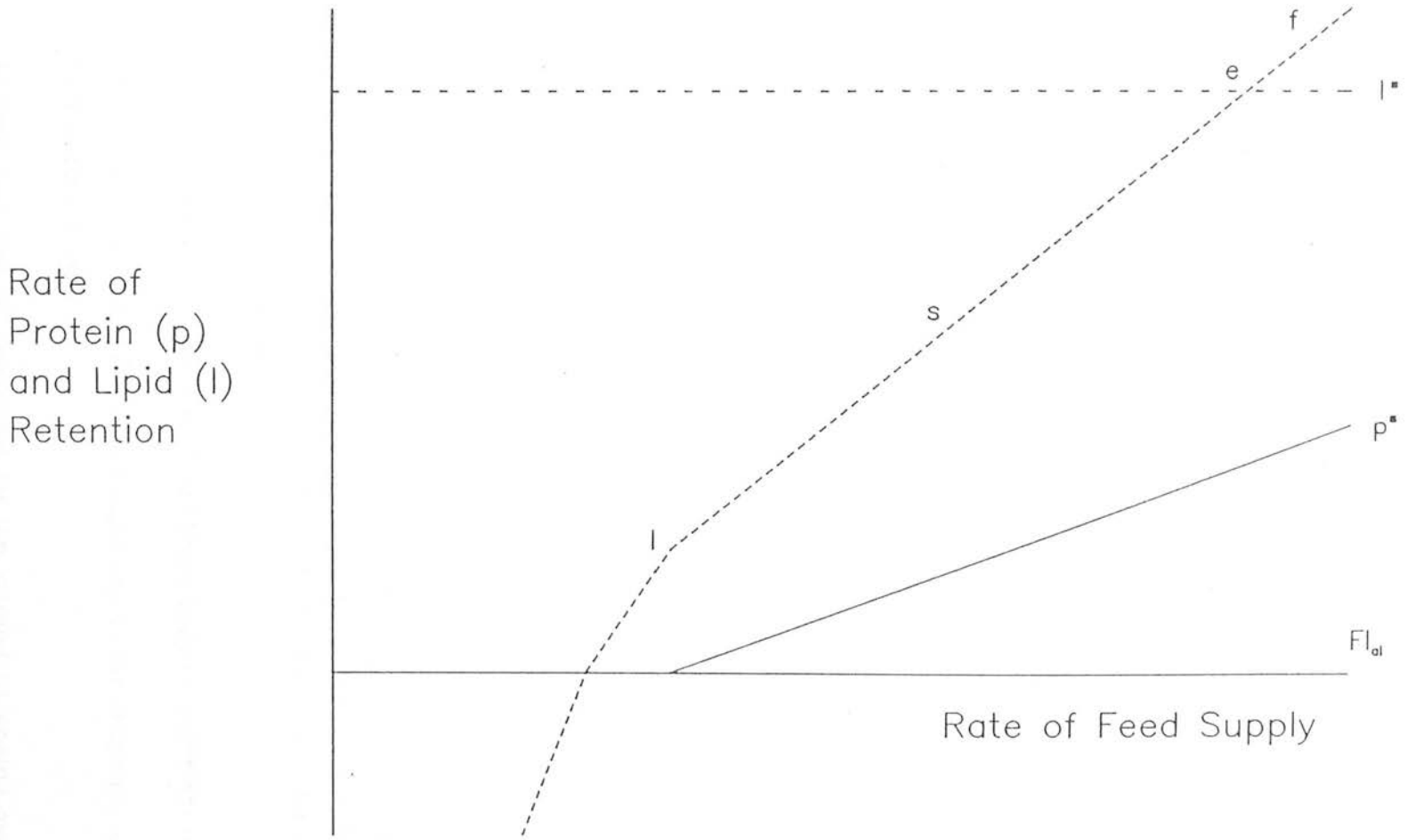


Fig. 3.2 Predicted Protein and Lipid Retention on Allowances of an Imbalanced (nutrient–poor) Feed

lipid storage and synthesis.

3) When an allowance of feed B no longer supports lipid gain, lipid gain will be dependent on the energy available to the lamb after the expenditure of energy for maintenance less the energy derived from mobilised protein. Rate of lipid gain will be a function of the energy supplied from mobilised lipid.

3.3.1.3 Allowances of an Imbalanced (nutrient-rich) Feed

Suppose that the lamb is now given a feed C, which has the same ME content as feed A,but a much higher nutrient: energy ratio (Fig. 3.3). *Ad libitum* access to feed C allows the lamb to grow at its potential rate (p^*) and lay down lipid at its desired rate (l^*), but the lamb must tolerate excess nutrient intake.

1) When an allowance of feed C below *ad libitum* is offered to the lamb

a) nutrient supply will remain adequate to support the potential rate of protein gain, p^*.

b) energy supply will fall below the requirement for l^*. Lipid gain will be dependent on the amount of energy available to the lamb after the expenditure of energy in the storage and synthesis of the non-limited protein gain. Rate of lipid gain will be a function of the energy cost of lipid storage and synthesis.

2) When an allowance of feed C no longer supports lipid gain

a) nutrient supply may still permit p^*.

b) lipid gain will be dependent on the amount of energy available to the lamb after the expenditure of energy in the storage and synthesis of the non-limited protein gain. Rate of lipid gain will be a function of the energy supplied from mobilised lipid.

3) When an allowance of feed C no longer supplies sufficient nutrient for p^*

a) protein growth will be reduced according to the efficiency with which the nutrient supply is used.

b) lipid gain will be dependent on the amount of energy available to the

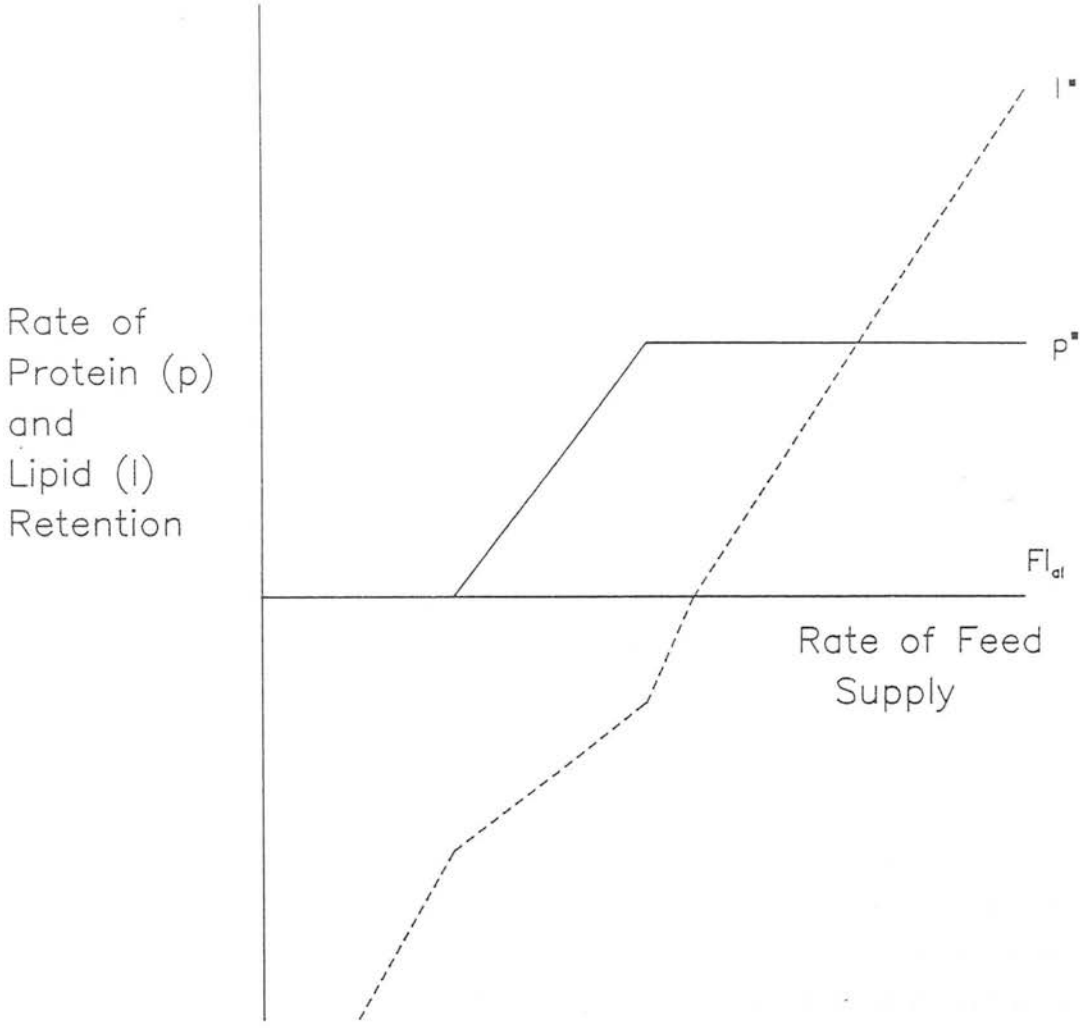


Fig. 3.3 Predicted Protein and Lipid Retention on Allowances of an Imbalanced (nutrient–rich) Feed

lamb after the expenditure of energy in the storage and synthesis of the limited protein gain. Rate of lipid gain will be a function of the energy supplied from mobilised lipid.

4) When an allowance of feed C no longer supplies sufficient nutrient for protein gain, lipid gain will be dependent on the energy for maintenance less the energy derived from mobilised protein. Rate of lipid gain will be a function of the energy supplied from the mobilised lipid.

The model generates a number of predictions which could be useful as a guide to understanding the measured responses of lambs to limiting conditions. Restricted allowances of the balanced feed A (Fig. 3.1) cause the lamb to grow protein below p^* and lipid gain below l^*. Allowances of the nutrient-poor feed B (Fig.3.2) cause the lamb to grow protein at a limited rate, but lipid gain may be faster (point f), equal to (point e) or slower than (point s) the desired rate l^*. Furthermore, the lipid: protein ratio of the gain on feed B will always be greater than the desired ratio. However, it will be noted that in the example chosen, feed B is grossly imbalanced since at the point of protein maintenance lipid retention is positive (point l) and *ad libitum* intake of feed B is much higher than that for feed A. Most imbalanced feeds offered to lambs would not be so extreme. In these cases, allowances of the feed may still cause the lamb to gain lipid faster than l^* but the lipid: protein ratio of the gain will fall. Finally, some allowances of the nutrient-rich feed C (Fig. 3.3) have the unique feature of supporting rates of lipid gain less than its desired rate, whilst permitting the lamb to grow protein at its potential rate, p^*.

The deductions from the theory therefore lead to the expectation that the data of published restricted feeding experiments, should all the conditions of the model be met, will belong to one of four kinds. A useful index for distinguishing the categories is to compare the response of restricted animals in terms of both protein growth rate and lipid: protein ratio of the empty body to that of animals grown at their potential rate with their desired body composition (see Chapter I). Thence, the four types of response become:

(i) *when protein growth rate is limited* and the lipid: protein ratio of the empty-body is greater than desired.

(ii) *when protein growth rate is limited* and the lipid: protein ratio of the empty-body is equal to that desired.

(iii) *when protein growth rate is limited* and the lipid: protein ratio of the empty-body is less than desired.

(iv) *when protein growth rate is non-limited* and the lipid: protein ratio of empty-body is less than desired.

The value of this theoretical framework is now determined by experimental test using existing data in the literature.

3.3.2 Case I - Protein growth rate limited; lipid: protein ratio greater than that desired.

Andrews and Orskov (1970a,b) fed each of five feeds, with different crude protein contents (100,125, 150, 175 and 200g crude protein/kg) at one of three levels (low, medium and high, the latter being close to ad libitum) to lambs of 15kg liveweight. Lambs on the medium allowance of the 100 and 125g CP/kg feeds had slower gains of protein, and had higher lipid: protein ratios, at the same protein weight, than lambs fed on the high allowance of the 175 and 200g CP/kg feeds. However, neither of the low-protein feeds used in the experiment were imbalanced enough in terms of protein: energy ratio to meet the conditions of the model. The outcomes of the experiment therefore undermine the assumption that protein: energy ratio of a feed for ruminants is independent of feeding level.

A second example of this type of outcome is found in the experiment of Meyer and Clawson (1964). Lambs, at an initial liveweight of 35kg (5.2kg protein) were offered a single feed containing 160g crude protein/kg either *ad libitum* or at 0.84, 0.68, 0.52, or 0.36 of *ad libitum*. The lambs fed *ad libitum* gained protein at a rate of 19g/day, whilst lambs on the 0.84 treatment, in the same period, gained protein at 4.8g/day. The lipid: protein ratio at 5.4kg protein weight was 1.15 and 1.39 for the *ad libitum* and 0.84 treatments respectively.

3.3.3 Case II - Protein growth rate limited; lipid: protein ratio equal to that desired.

The feeds and methods of restriction in the papers of Reid (1968), Burton and Reid (1969), Andrews and Orskov (1970) and Searle and Graham (1982)

reduced the protein growth rate of the restricted lambs compared with *ad libitum* or better-fed controls but did not alter the lipid: protein ratio of the empty-body at the same body protein weight. Palsson and Verges (1952), Morgan and Owen (1972a) Kemp *et al* (1976) and Murray and Slezaceck (1976) published similar results in terms of the ratio of carcase fat to carcase muscle, and rates of carcase muscle deposition.

The slower growing lambs in each of these cases could have been limited by nutrient supply in their growth of protein, and the energy consumed surplus to their requirements for maintenance and growth would then have been sufficient during the restriction period, up to the point of slaughter, to support a net gain of fat giving a similar lipid: protein ratio to the faster growing lambs at the same weight of protein. Doubts over the assumption that nutrient: energy ratio is not affected by feed restriction could also partially explain these outcomes.

Such findings have lent support to the opinion that the body composition of sheep cannot be altered by a feed restriction. In the context of the present review, this conclusion shows itself to have been deduced from the outcome of a particular case of the set of possible types of feed restriction.

A knowledge of the path of growth and fattening of a sheep in fulfillment of its inherited growth-plan, as described in Chap. I, indicates a number of circumstances which promote the possibility of a feed restriction failing to affect body composition. The experiments quoted above failed to shift substantially the lipid: protein ratios of the restricted sheep but took as their subject, with the exception of Burton and Reid, lambs which did not exceed 4kg of body protein, or 8kg of carcase muscle. The desired pattern of fattening lambs (Chap. I) showed that it is only beyond protein weights of about 4kg that the lamb's gain of lipid is most appreciable relative to its protein growth. It is therefore a weak test of the theory that body composition is not affected by feed restriction to take lambs of less than 4kg protein weight, impose mediocre feed restrictions upon them and then pronounce that the theory is supported by the statistically non-significant data. The numbers of lambs and the severity and length of treatments used in experiments ought to be sufficient to permit potential treatment effects to show despite the natural variation within a breed and the disadvantage of small litter size in sheep. In this way, the possibility that a feed restriction does influence the body composition of lambs

could be sternly tested, in principle, before deciding whether the effect is achieveable under commercial conditions or of economic significance.

3.3.4 Case III – Protein growth rate limited; lipid: protein ratio less than that desired.

The thorough investigation made by Andrews and Orskov (1970a,b) provides further published data with which to test the idea that certain allowances decrease both the protein growth rate and the lipid: protein ratio of lambs.

In the medium treatments of the 175g and 200g CP/kg feeds offered rates of protein retention were slower than those for the lambs fed close to *ad libitum* on the 200g CP/kg feed. At the 40kg slaughter point, the two restricted treatments quoted had lower, but probably not significantly lower, lipid: protein ratios than the *ad libitum* fed lambs.

Boccard and Duplan (1961) showed a similar effect in lamb growth and body composition from birth to 35kg liveweight between their high growth rate treatment group (350g/day) and their low growth rate treatment group (250g/day) but did not carry out a serial slaughter study which leaves the results difficult to interpret.

Beyond the evidence for this effect on sheep, the classical studies of McMeekan (1940), on pigs, may be cited as an example of a reduced muscle growth rate with depleted fat: lean ratio following a feed restriction. McMeekan's 'low-plane' pigs were fed in such a way to show these responses compared with 'high-plane' (*ad libitum* fed) pigs.

3.3.5 Case IV – Protein growth rate non-limited; lipid: protein ratio less than that desired.

Confirmation of this proposition would be of importance to animal production, in that it offers the possibility that lambs may be reared under feeding regimes which allow maximum protein growth rate to be achieved, thereby minimising the maintenance cost of production, whilst avoiding the deposition of excess, unwanted fat, penalised financially under current market conditions (Croston and Pollott, 1985).

Unfortunately, there is only one reference in the literature to support this expectation of the theory. The paper of Lloyd *et al* (1985) reported that Suffolk X Greyface wether lambs offered 1kg/day of a feed supplying 140gCP and 11.2 MJME reduced their rate of lipid gain without limiting their rate of protein growth. However, it is not doubted that animals can become less fat, as illustrated in the sheep by ram 8667 of Blaxter, *et al* (1982) which had 0.5kg of lipid at a protein weight of 9.22kg. Fully-fed counterparts had over 40kg more lipid at the same protein weight. However, the path by which this body state was reached had not been recorded by comparative slaughter or nitrogen balance techniques. It cannot, therefore, be used as evidence to support the theory.

Such a substantial discrepancy between a theory and its associated facts provides grounds on which to challenge the validity of the theory. Nevertheless, the theory has stipulated that the allowance be non-limiting in nutrients, which prompts enquiry into the manner in which feed restrictions have been most commonly brought about in the published experiments.

In the experiments reported by Meyer and Clawson (1964), Burton and Reid (1969), Andrews and Orskov (1970), Morgan and Owen (1972) and Drew and Reid (1975) the feeding scale used was one which varied as the animals increased in liveweight. Therefore, it is difficult to decide whether and when a nutrient was limiting to growth.

McMeekan (1940), Palsson and Verges (1952) and Murray and Slezaceck (1976) fed some of their animals on 'high-plane' treatments in which the quantities of nutrients in the feed were shown to be adequate to support high rates of muscle gain. The 'low-plane' treatments were implemented by offering a smaller quantity of the same feed given to the 'high-plane' animals. Consequently, the low-plane animals received not only a lower energy allowance but were also limited in nutrient supply. If protein growth is to proceed at its maximum rate when the animal is given a feed allowance, the nutrient content of the feed must be made sufficiently high, which may involve the feed having an abnormal composition, to ensure an adequate supply even from small allowances. The difficulties of predicting the protein yield of feed allowances for ruminants has been discussed previously and remains a problem in this context.

3.4 Comments on the Design of Restricted Feeding Experiments

The limitations mentioned in the method of testing key propositions in the theory of the growth of animals when poorly fed encourage a search for a more rigorous design for restricted feeding experiments. The inquiry takes as a guide the ideas proposed by Parks (1982) and Taylor, Turner and Young (1981) but begins by addressing the contrasting relationship between the rate of feed intake and the state of the animal in restricted and *ad libitum* feeding experiments.

It was proposed in Chapter II that the *ad libitum* feed intake of an animal arises from the desire of that animal to fulfill its growth-plan. The desired rate of feed intake was asserted to be dependent on the size and state of the animal. The achieved, *ad libitum* feed intake was then a product of the desired feed intake and the character of the feed in terms of its nutrient balance, its bulkiness and its toxicity.

When an animal is restricted in its feed intake, the desired feed intake can no longer be satisfied, and the view has been adopted that the animal partitions the nutrient and energy resources which it receives according to certain rules. The growth of the animal in this instance becomes dependent on the nature of the feed allowance, that is, the rate of feed intake.

If feed intake in a restricted feeding situation is looked upon as an independent variable, it follows that an acceptable design for a restricted feeding experiment should allow feed intake to be a quantity which is easily reckoned and which has the same magnitude for individuals on a given treatment. Experiments which adjust feed intake for the individual, according to a scale of liveweight, fail on both accounts. The response to a feed restriction in terms of the dependent variable, growth, is not strictly comparable between individuals within a treatment let alone between treatment groups, when the independent variable, feed intake, differs for each individual in the experiment.

One way to avoid such difficulties in design is to offer the feed allowance to the animal at a fixed rate, as was done in the work of Searle, Graham and O'Callaghan (1972) and Thompson and Parks (1983), to which an added refinement is to allow the animal to enter the period of restriction in its desired state, by giving the allowance to the animal before the *ad libitum* feed

intake exceeds that of the restriction (Taylor *et al* ,1981). These workers also suggested that the same quantity of any amount of feed refused by an individual during, say, a period of illness, should be given back at a later date in order to make the total feed intake exactly equal for animals on a single treatment. The style of such a design is represented graphically in Fig. 3.4.

According to the nature of the allowance, the animal is expected to respond in one of the four ways outlined above. Up to the moment of feed restriction (t_1 or t_2, Fig 3.4) the allowance was supplying at least enough nutrient to support the potential for growth. Once under a restriction in feed supply, the animal, depending on its size, might past firstly through a phase of lipid retention until the energy yield of the allowance becomes limiting to growth, at which point the animal begins to lose lipid. In time the animal is expected to lose all its reserves of lipid in order to augment its energy supply for growth. When the animal has no more lipid reserves and growth has ceased because it is limited by energy supply, the allowance maintains the animal in the lipid-free state which is known as an immature equilibrium weight (Taylor *et al*, 1981).

An important feature of the feed intake at an immature equilibrium is that it reflects, by definition, the maintenance requirement of an animal at a given degree of maturity, Pt/Pm. Consequently, Taylor used this method with cattle to determine that the relationship between degree of maturity and rate of feed intake is described by a simple linear function. Parks (1982) then described the boundaries of the relationships between degree of maturity (u) and the rate of feed intake (dF/dt) in what he called the Growth Phase Plane (GPP), presented in Fig. 3.5 where the passage of time is implicit.

The plane is bisected by Taylor's Diagonal, which shows the linear relationship between u and maintenance dF/dt on a given feed. Above the Diagonal lies the region of feed allowances which leave the animal in a state of semi-starvation. The y-axis represents complete starvation at any degree of maturity (Fig. 3.5). The response of an animal to very poor feeding has not been addressed in this Chapter and whilst it may be of importance for animal production in countries which experience extremes of climate to answer the scientific questions raised by submaintenance feeding, the occasion of starvation of an animal is not desirable from either an ethical or agricultural standpoint.

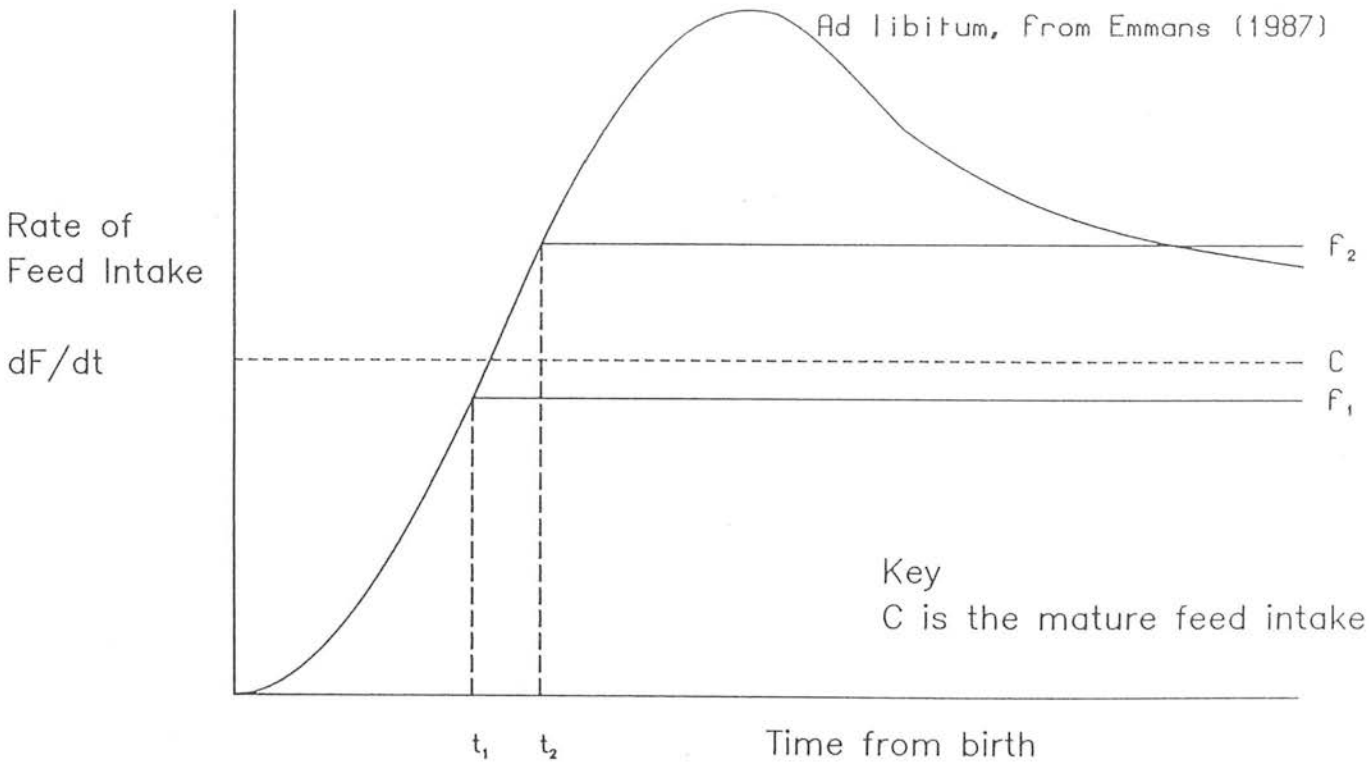
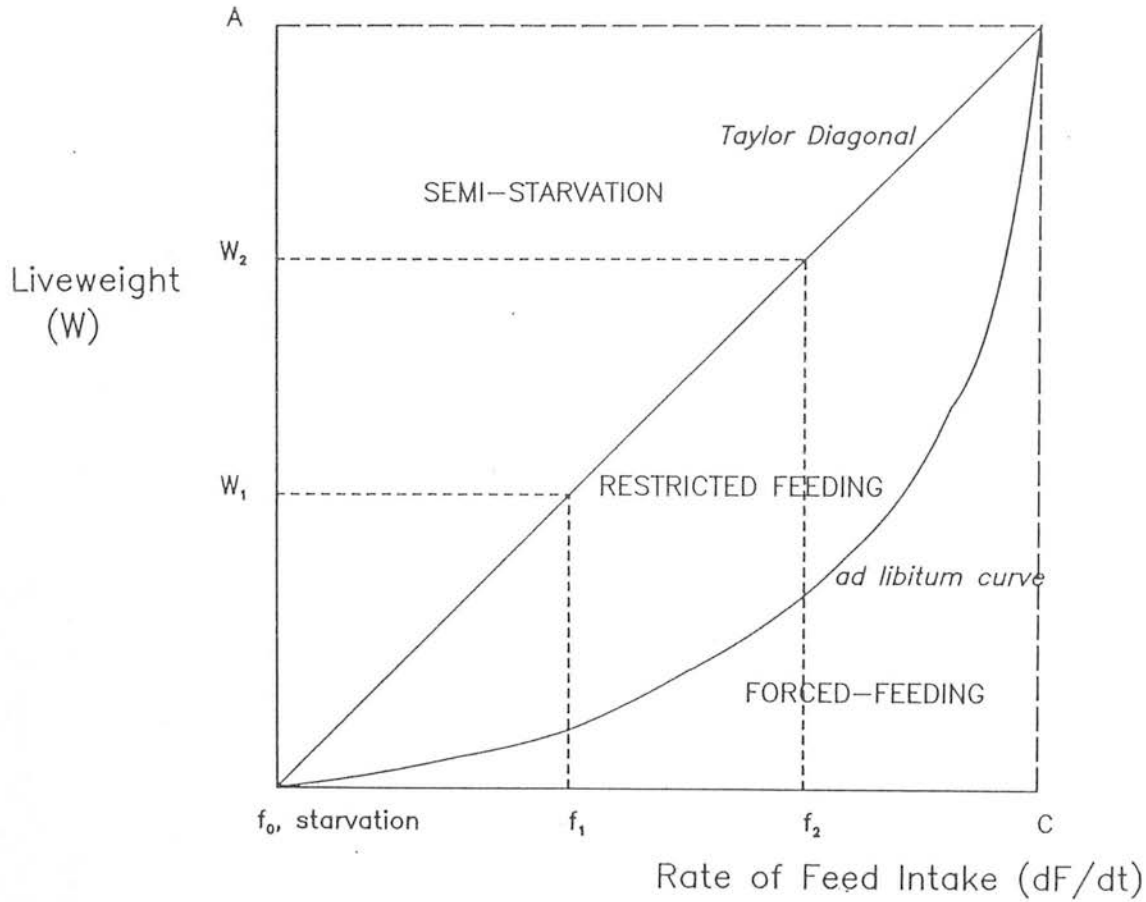


Fig. 3.4 The Relationship between Rate of Feed Intake and Time for Sheep – with a suggested design for a restricted feeding experiment.



KEY
A = mature liveweight
C = mature feed intake

[Figure based on that of Parks (1982), Ch.5]

Fig. 3.5 The Relationship between Liveweight and Rate of Feed Intake in Parks' Growth Phase Plane (GPP)

Below the Diagonal the animal is eating above its maintenance level, and is either restrained (line R) by feed restriction or by feed constraint, or not (line AL) from meeting its *ad libitum* feed requirement. Above the AL line is the domain of forced-feeding experiments which are judged to yield no valuable insight into the natural behaviour of animals. Within the boundaries of restricted feeding experiments, the GPP illustrates how animals, given fixed rates of feed intake (f1; f2) below C, the mature rate of feed intake, gradually acquire immature equilibrium weights (W1; W2 respectively). Such experiments are deemed to provide data which are readily analysable and comprehensible in the light of a suitable theory.

3.5 Experiment IV : A Test of the Theory of Growth under Restricted Feeding Conditions

3.5.1 Objectives

The chief purpose of this experiment was to provide the feeding conditions considered to be necessary for a categorical test of the assertion (3.3.5) that there is a set of feed restrictions which allows a lamb to grow protein at a non-limited rate whilst gaining lipid below its desired rate. The opportunity was also taken to re-examine other areas of the theory, particularly the proposition that protein growth rate can be slowed without influencing the lipid: protein ratio.

3.5.2 Propositions

The experimental propositions fell into three categories according to whether (a) the feed was offered *ad libitum*, (b) the energy allowance was first limiting to desired lipid gain or (c) the protein allowance was first limiting to growth.

Propositions [1(A) - 3(A)]

Lambs given *ad libitum* access to a single feed which is not first limiting in a nutrient (protein) will:

P1(A): grow protein at the rate of their potential

P2(A): gain lipid at their desired rate. Hence their lipid: protein ratio will be the desired ratio.

P3(A): maintain the form of the lipid-free empty body in accordance with their inheritance.

Propositions [1(B) - 7(B)]

Lambs given a restricted allowance which provides enough protein to suport non-limited growth will allocate their scarce energy resource to:

P1(B): grow protein at the rate of their potential.

P2(B): gain lipid at a rate determined by the energy yield of the allowance and the energy requirements for maintenance and growth. Consequently, the lipid: protein ratio will fall below the desired level.

P3(B): maintain the form of the lipid-free empty body (excluding feed-processing organs and gut-fill) in accordance with their inheritance.

P4(B): show a smaller increase in their feed-processing organs (stomachs, intestines and liver) :muscle ratio than fully-fed counterparts.

P5(B): show a smaller increase in their gut-fill: muscle ratio than fully-fed counterparts.

P6(B): gain liveweight at a slower rate and have a lower feed conversion ratio (g feed intake per g gain) than fully-fed counterparts.

Propositions [1(C) - 7(C)]

Lambs given a restricted allowance which provides insufficient protein to support non-limited growth, will allocate their scarce protein resource to:

P1(C): grow protein at the fastest rate permitted by the allowance of protein. This rate of growth will be below the potential rate.

P2(C): gain lipid at a rate determined by the energy yield of the allowance and the energy requirements for maintenance and (the restricted) growth of protein, i.e. the lipid: protein ratio need not fall below the desired level.

P3(C): maintain the major form of the lipid-free empty body.

P4(C): show a slower increase in their feed processing organs (FPO): muscle ratio.

P5(C): show a slower increase in their gut-fill (GF): muscle ratio.

P6(C) gain liveweight at a slower rate and have a higher feed conversion ratio than those not first limiting in a nutrient.

3.5.3 Materials and Methods

Feeds Two pelleted feeds were designed to have different crude protein (CP) contents and to have similar yields of metabolisable energy (ME). Consequently, feed LP, containing 140g CP/kg freshweight (FW) and feed HP, containing 220g CP/kg FW, were formulated using barley, maize, soya bean meal and hay (Table 3.1) so as to have similar ME yields of 11.7 and 11.9 MJ/kg FW respectively. The chemical analysis of the two feeds is given in Table 3.2. To ensure a daily supply of minerals and vitamins, a proprietary [14] sheep mineral mix was fed separately to the lambs (see Management).

Animals Seventy-three Scottish Blackface wether lambs, which had a mean birthweight of 3.8kg (s.d 1.7) were abruptly weaned at an average age of 51 days (s.d. 4). The lambs had been reared as twins on their dams. The latter had been in receipt of a predominantly ryegrass sward with a height in excess of 5cm, throughout lactation. The mean weaning liveweight (LW) of the lambs was 18.2kg (s.d. 2.2). The average growth rate from birth to weaning had therefore been 281g/day (s.d. 33)

Management The lambs were housed in a naturally ventilated, slatted shed. Each lamb was penned individually. The fluorescent lighting of the shed was scheduled to augment natural light so as to give no less than 20 hours of light to the lambs from midsummer onwards. The liveweight of the lambs was recorded twice weekly at 1300h on an Avery mechanical weighing platform (100kg X 0.2kg). The allowances of feeds and minerals, weighed on a Avery mechanical balance (2kg X 5g) were administered to the lamb daily commencing at 800h. Refusals were recorded on Mondays, Wednesdays and Fridays. It was not possible to record spillage losses but these had not been observed to be appreciable in previous experiments under similar conditions. An equivalent weight of fresh feed to that refused by the lambs on the restricted allowances was given back as soon after the day of refusal as possible, usually a day or two later. The lambs given feed AL were always provided with enough feed to ensure a refusal of 10-15%. These lambs were also given free access to the mineral supplement in a separate trough which

[14] Colborn Dawes Intensive Sheep Mineral and Trace Element Mix (low magnesium and low phosphorous content).

Table 3.1 The Composition of the Feeds (g/kg freshweight) in Experiment 4

Ingredient†	Feed LP	Feed HP
Hay	150	150
Soya bean meal	110	330
Flaked maize	340	220
Ground barley	350	250
Molasses	50	50
	1000	1000

† vitamins and minerals fed separately

Table 3.2 The Chemical Analysis of the Feeds (g/kg freshweight) in Experiment 4

Constituent	Feed LP	Feed HP
Crude protein (CP)	147	224
Crude fibre	86	91
Ether extract	24	22
Ash	35	44
Dry matter	872	872
Metabolisable† energy (MJ)	11.7	11.9

† calculated from feed tables

was replenished daily.

Design Each feed was offered *ad libitum* (AL) and at fixed, daily rates of 1.2kg and 0.8kg FW. By this method, it was possible to measure the response to a comprehensive set of inter-related allowances (Table 3.3).

Slaughter Schedule The slaughter schedule was designed to yield maximum information concerning changes in liveweight composition by spreading the slaughterings over a wide range of liveweights instead of providing fewer, more precise estimates at a fixed point. Such a dispersed design suited the recommended method of allometric analysis (Chap.1) since all the body composition data contribute to the tests of linearity in the relationship and of closeness to the expectation.

An initial slaughter group of 6 lambs included the heaviest and lightest lamb from the experimental population and four others, picked at random from four weight categories to represent the range of liveweights between the two extremes.[15] Thereafter, lambs were slaughtered at 5kg intervals up to a final liveweight (dependent on the treatment) no more than 200 days from the beginning of the experiment. The schedule is given in Table 3.4.

Slaughter and Physical Dissection Procedures When a lamb reached a liveweight close to its intended slaughter wieght, it was weighed daily until its liveweight was within 0.5kg of target for two days consecutively. Provision for its slaughter was then made the following day.

On the day of slaughter, the lamb was fed as usual, then shorn mid-morning and the weight of wool recorded. At 1245h (as close to the usual weighing time as possible) the lamb was weighed and transported immediately to the slaughtering facilities one mile distant.

The lamb was stunned with a shot from a captive bolt pistol, and the blood vessels of the neck severed. The draining blood was collected. The lamb's body was then dissected into the following components:

--head

[15] The purpose of this exercise was to acquire the widest possible data source for estimating initial body composition in the test lambs from regression analysis of components on liveweight of the intial slaughter group.

Table 3.3 The Design of Experiment 4

Treatment	n	Feed allowance (kg/day)	Feed	CP allowance (g/day)	ME allowance (MJ/day)
Initial Slaughter	6	-	-	-	-
T1	8*	*ad libitum* (AL)	HP	non-limiting	
T2	8*	*ad libitum* (AL)	LP	non-limiting	
T3	12	1.2	HP	269	14.3
T4	13†	1.2	LP	176	14.0
T5	14†	0.8	HP	179	9.5
T6	12	0.8	LP	118	9.4
total	73				

* 4 male-male twins from same dam

† includes 6 male-male twins from same dam

Table 3.4 The Slaughter Schedule of Experiment 4

Treatment	T1	T2	T3	T4	T5	T6
Liveweight (kg)	Initial	ALHP*	ALLP*	1.2 HP	1.2 LP†	0.8 HP†	0.8 LP
14-24	6	-	-	-	-	-	-
25	-	-	-	2	2	2	2
30	-	2	2	2	2	2	2
35	-	-	-	2	2	4	2
40	-	2	0	2	2	2	2
45	-	-	-	2	2	-	-
final	-	4	3	2	3	4	3
Total	6	8	5[d]	12	13	14	11[d]

*, † male-male twins slaughtered at same liveweight

d treatments which incurred losses

--heart
--lungs and trachea
--liver and gall
--spleen
--reticulo-rumen
--intestines
--omental and mesenteric fat (caul)
--feet[16]
--warm carcase (including kidneys)

Organs weighing over 300g were weighed on a Souter Electronic weighing platform (12kg X 1g), smaller organs on an Avery weighing scale (500g X 1g). The stomachs and intestines were weighed full, stripped of their contents and then weighed empty. Gut-fill was calculated by difference.

All non-carcase components, excluding the gut-fill and horns were placed in a double sealed plastic bag and stored at -20°C.The warm carcase, half of which was to be jointed and dissected into muscle, bone and fat, and half used for chemical analysis, was chilled at 4°C and dissected within two days.

Dissection of the Cold Carcase The cold carcase of the lamb was split, and the left side jointed and dissected in accordance with the guidelines set by the Meat and Livestock Commission for retail jointing and tissue separation (see Appendix E). The dissection provided measurements of muscle, bone, sub-cutaneous, intermuscular and kidney knob and channel (perirenal) fat tissues in commercial joints of carcase.

Chemical Analysis of the Cold Carcase and Non-carcase Fractions The right (undissected) side of the carcase and the non-carcase fractions were prepared separately for chemical analysis. Two homogeneous 200g samples of both fractions for each sheep were obtained by a preliminary crushing through a prebreaker (Henry Balfour & Co. Ltd.) followed by two passes through a Wolfking mincer, fitted with a 10mm and then a 5mm plate.

A limitation in the laboratory facilities available meant that individual samples for both fractions could not be accepted as planned. Consequently, it was decided to pool samples from individuals of the same treatment which were slaughtered at the same liveweight. The identification numbers of the

[16] Forelimbs cut at metacarpal and hindlimbs at metatarsal joints.

pooled lamb samples are given in Appendix F. The pooled carcase and pooled non-carcase sample for each lamb-pair was obtained by proportionate sub-sampling of the original individual carcase or non-carcase sample according to the weight of the fraction. This procedure ensured a representative sample for the lamb pairs.

The samples were taken to the laboratory for analysis of

(i) dry matter by drying to constant weight at 105°C, and in the dry matter

(ii) nitrogen content by a macro Kjehldahl procedure with crude protein calculated as 6.25 X nitrogen.

(iii) lipid content by Soxhlet extraction with 60-80°C petroleum ether for 8 hours.

(iv) ash content by burning in a muffle furnace at 600°C to constant weight.

(v) gross energy value by adiabatic bomb calorimetry.

It was only considered necessary to repeat analysis of dry-matter on samples 1387/1538 and the repeat measures are those used to calculate the values of the chemical components in Appendix F.

Method of Data Analysis The reduced number of chemical analyses for estimating protein weight weakened the analysis of the protein growth curve when it was calculated directly as protein weight (of an individual in a treatment) against time. Each estimate of protein weight stood in isolation from the others and, hence, no assessment of possible outliers could be made. Estimates of initial protein weight were also prone to error and the pooling of samples meant that many points were related.

Consequently, it was suggested that most of these faults would be overcome by fitting a smoothing function (chosen for goodness-of-fit) for each treatment to the data on the graph of protein content of the LW at a LW. The work of Blaxter *et al* (1982) gave reason to expect that the relationship for *ad libitum* fed lambs would be a simple power function of LW, that is $LW^{-0.25}$. With the restricted animals, however, no particular relationship was anticipated and so a best-fit polynomial was to be used to describe the data. Then, from a knowledge of both initial and slaughter LW, protein weight could be

back-calculated, transformed by the rearranged Gompertz equation (Chap. I) and the rate parameter, B, for each individual estimated using the known time to slaughter. The method of LW measurement meant that there would be an acceptable degree of certainty in the accuracy of these values.

3.5.4 Results

The data from three lambs have been excluded. Lamb 8 on treatment 6 died in week 2 because it failed to eat. Lambs 15 and 69 on treatment 2 had an excessively long period of feed refusal following the incidence of foot rot in week 16. The data of other lambs kept around that period are retained since the individuals were either slaughtered before their intended slaughter weight or were unaffacted by the disease.

Since it was a feature of the design that the feed restriction from the 1.2 treatment should occur at a later time (and thus, higher LW) than from the 0.8 treatment, the relative severity of the restrictions, compared with *ad libitum* feed intake, is illustrated in Fig. 3.6. The ALLP lambs were slower to take to their feed and tended to have lower feed intakes than ALHP lambs but these differences were not significant. Subsequently, the lambs established themselves on their treatments as planned. The dip in feed intake in the restricted treatments corresponds to the feed refused whilst the lambs had the foot infection. The same amount of fresh feed, as was refused, was restored in subsequent weeks.

P1: Protein Growth Rate The functions used to describe the decreasing proportions of protein in the LW of the treatments are given in Fig. 3.7. Using the method outlined above, and a P_m value of 7.5kg, estimates of B, the Gompertz rate parameter for protein growth, could be calculated and these are presented in Table 3.5.

The two AL treatments were not significantly different ($p > 0.1$) from each other and gave, collectively, a B^* value of 0.0176 which agrees closely with the B^* value for muscle growth (0.0173) given in Chap. I, the best estimate available of the expected growth rate of these lambs.

The 1.2HP treatment lambs had a B value of 0.010 (s.e. 0.0004) which was not significantly different ($p > 0.1$) from the expectation that their growth rate

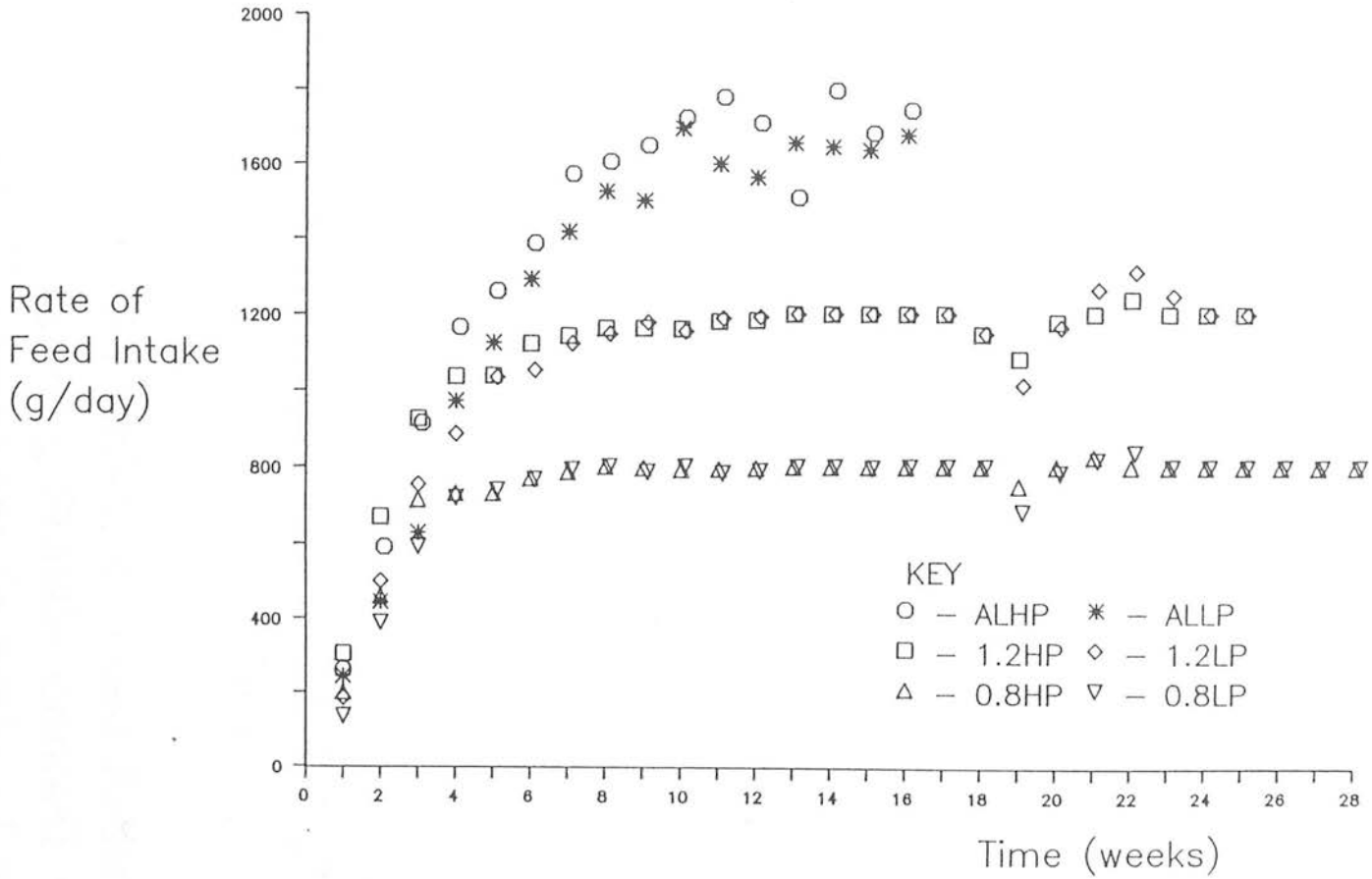


Fig. 3.6 The Pattern of Feed Intake of the Scottish Blackface wethers in Experiment 4

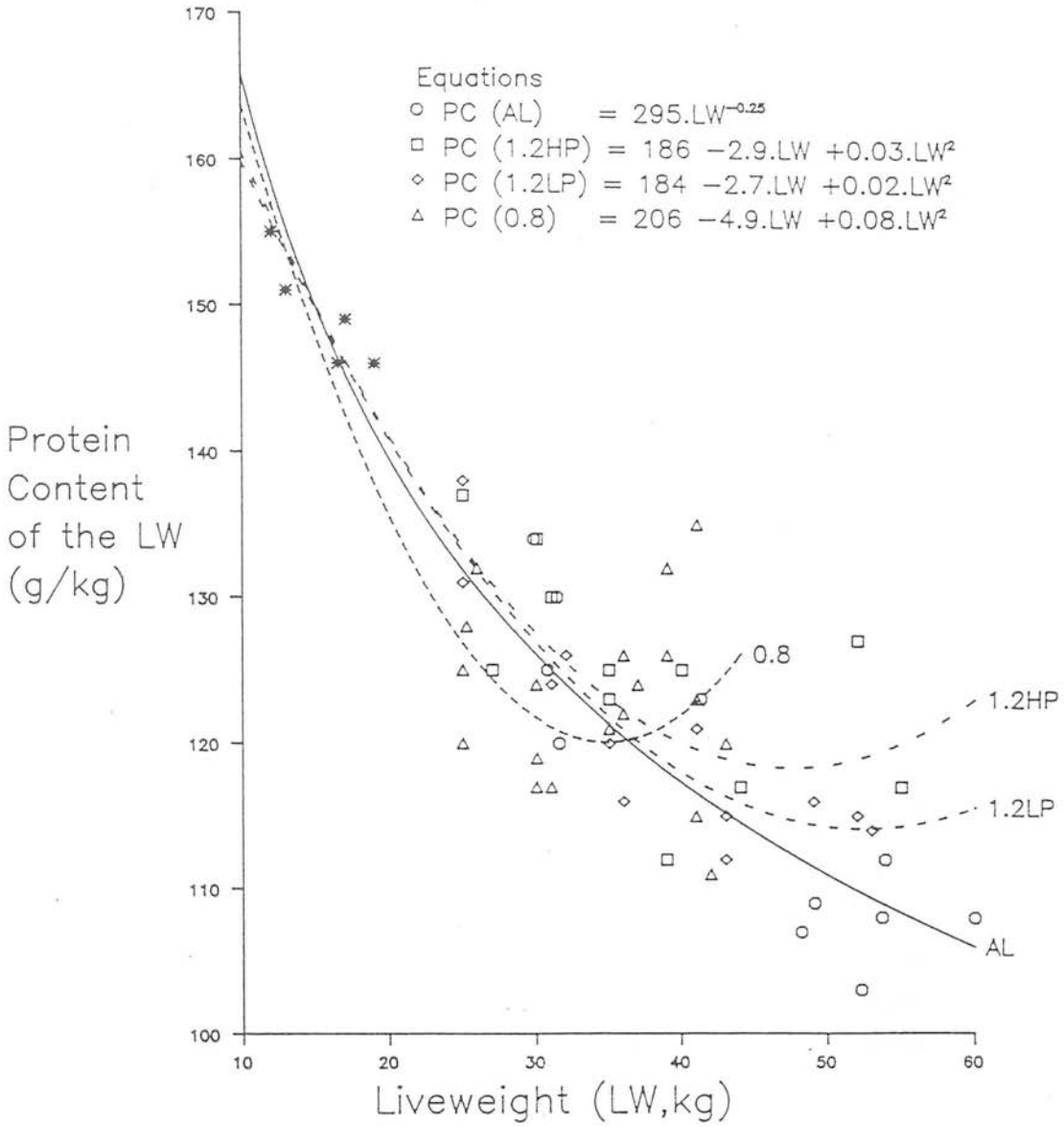


Fig. 3.7 The Effect of Feed Restrictions on the Protein Content of the Liveweight (g protein/ kg LW) in Scottish Blackface wethers

Table 3.5 The Effect of treatment on the Estimate of the Gompertz rate parameter (B) for Protein Gain

Treatment	n	B ($x10^{-3}$)	s.e. ($x10^{-3}$)
ALHP	8	10.58	0.44
ALLP	5	9.62	0.24
1.2 HP	12	10.00	0.45
1.2 LP	13	8.03	0.26
0.8 HP	10	5.31	0.48
0.8 LP	11	5.19	0.21

Table 3.6 The Effect of treatment on the Estimate of the Gompertz rate parameter (B) for Lipid Gain

Treatment	n	B ($x10^{-3}$)	s.e. ($x10^{-3}$)
ALHP	8	7.49	0.30
ALLP	5	6.86	0.13
1.2 HP	12	6.14	0.20
1.2 LP	13	5.16	0.18
0.8 HP	10	3.50	0.32
0.8 LP	11	3.38	0.16

would be similar to that of AL lambs (0.010,s.e. 0.0003). 1.2LP lambs, however, had a B value of 0.008 (s.e. 0.0003) which was significantly lower ($p < 0.001$) than that of the 1.2HP and AL lambs, which outcome went against expectations.

The 0.8HP lambs also had a B value (0.005, s.e. 0.0005) which was significantly lower ($p < 0.001$) than expected, that is than AL lambs. The B value for the growth of 0.8LP lambs (0.005, s.e. 0.0002) did not differ significantly ($p > 0.1$) from the expectation that it would be slower than 1.2 and AL lambs. The unexpected depression in growth rate of 0.8HP lambs, however, meant that the two 0.8 treatments did not differ significantly ($p > 0.1$).

P2: Rate of Lipid Gain The known allometry between lipid and protein in the chemical body permitted a similar analysis to the above to be carried out for estimating lipid growth rates in the AL lambs. Although the same model would not be expected to suit the restricted treatments, it may be fitted as a first step to testing if lipid growth rate deviates in the 1.2 and 0.8 treatments from that of the AL lambs. Using a mature lipid weight of 32kg estimates of b (the rate parameter for the lipid growth curve) were made and are presented in Table 3.6.

The b values for lipid gain of the AL lambs were not significantly different ($p > 0.1$) from each other, and had a collective b^* value of 0.0183 which was close to the B^* value for protein indicating adherence to the allometric model.

The 1.2HP lambs were expected to have a lower b value for lipid gain than AL lambs; their b value of 0.006 (s.e. 0.0007) was significantly lower ($p < 0.001$) than that of the AL lambs. 1.2LP lambs (0.005, s.e. 0.0007) had an unexpectedly lower ($p < 0.01$) b value for lipid gain than 1.2HP lambs, but showed the expectedly greater value ($p < 0.001$) than 0.8HP lambs (0.004, s.e. 0.0003). As a consequence of their depressed rate of protein growth, 0.8HP lambs did not differ significantly ($p > 0.1$) in their b value for lipid gain than 0.8LP lambs (0.003, s.e. 0.0005).

The effect that the relative differences in growth of protein and gain had on the ratio of lipid: protein in the lambs is presented graphically in Fig. 3.8 as the natural logarithm of lipid weight against the natural logarithm of protein weight. The regression of the AL treatment group had a slope of 2.39 (s.e.0.19) which was of a similar form to that expected from Chap. I.The 1.2HP group (2.28, s.e.

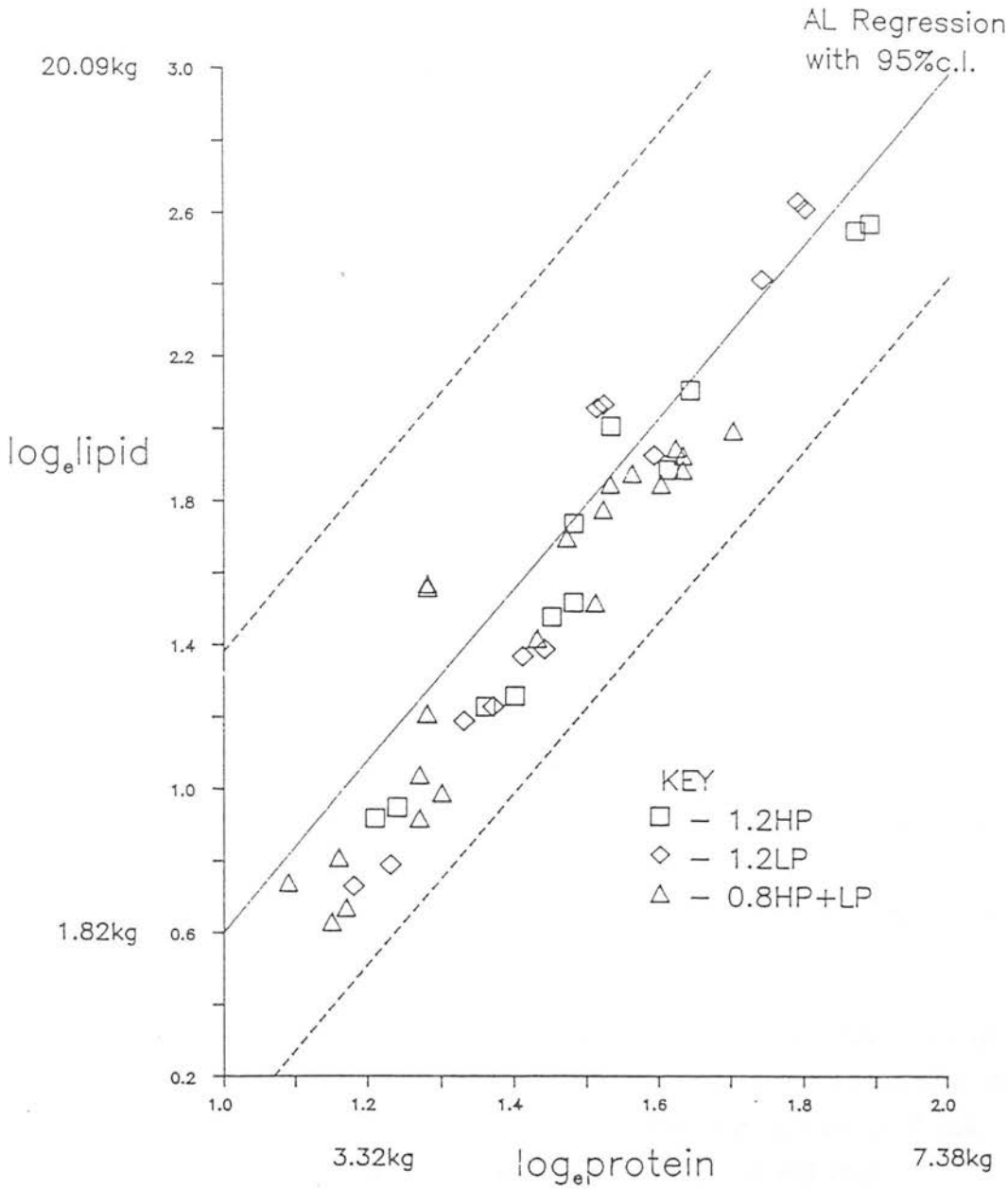


Fig. 3.8 The Effect of Feed Restrictions on the Allometric Relationship between Lipid and Protein in Scottish Blackface wethers

0.11) gave no evidence of a statistically significant ($p > 0.1$) reduction in their lipid: protein ratio compared with the AL group despite the recorded differences in the b value for lipid gain. The data points do, however, lie consistently below the regression line for the AL lambs, and drift upwards at higher degrees of maturity. The 0.8 treatment group also showed a consistent lie beneath the AL standard, and had a significantly lower slope value ($p < 0.01$) of 2.04 (s.e. 0.13).

P3: The Form of the Lipid- and Fat-free Empty Body The allometric plot of water on protein was used as a first test of the expected similarity between treatments in the form of the lipid-free empty body. No differences were found in the allometric relationships between treatments and the pooled regression.

ln water = 1.48 + 0.866 ln protein (s = 0.046)

was not significantly different ($p > 0.25$) from the expected relationship of Chap. I. Similar analysis of the allometry of the ash component cast doubt on the suitability of the samples for ash analysis. Small uncrushed fragments (c. 5mm) of bone had been present in the sample and had adversely affected the accuracy of the measurement. The data are given in Appendix F.

Further analysis of the fat-free empty body (FFEB), by allometry on carcase muscle, was undertaken. The expectation, and confirmation, that there were no significant differences ($p > 0.25$) between the HP and LP groups within a feeding level permitted the presentation and analysis of the data to proceed using pooled AL, pooled 1.2 and pooled 0.8 treatment groups.

The allometric plots of bone: muscle showed no significant differences ($p > 0.1$) in slope between AL lambs (0.632, s.e. 0.037), the 1.2 lambs (0.622, s.e. 0.049) or the 0.8 lambs (0.677, s.e. 0.043) and the expectation of 0.694. A similar pattern of outcomes applied in the analysis of pluck and feet.

The allometric plots of head: muscle also showed no significant differences ($p > 0.1$) between AL lambs (0.718, s.e 0.051) and the 1.2 lambs (0.686, s.e. 0.045) and the expectation of 0.672. However, the 0.8 treatment group (0.757,s.e. 0.043) showed that they had a significantly greater ($p < 0.05$) relative growth rate of head than the pooled AL/1.2 lambs.

Regression analysis of the allometric relationship between pelt (skin + fleece) and muscle revealed no significant differences ($p > 0.1$) between 1.2 and 0.8 treatments and the expected slope of 1.26, but the AL value was significantly lower ($p < 0.01$). Therefore, within the experiment, both 1.2 (1.28, s.e. 0.072) and 0.8 (1.23, s.e. 0.075) treatment groups were shown to have significantly greater ($p < 0.001$) relative growth of pelt than AL lambs (0.93,s.e. 0.084). However, the shearing of the lambs at slaughter permitted a further test of whether pelt differences were attributable to differences in wool weight. Regression analysis of the allometric relationship between unwashed wool [17] on body protein disclosed no significant differences ($p > 0.1$) between treatments and a common relationship of the form:

$$\ln \text{wool} = -2.92 + 2.09 \ln \text{protein} \quad (s = 0.238)$$

P4: Gain of Feed Processing Organs (FPO) In the absence of any anticipated form to the relationship between FPO weight and muscle weight, simple linear models were favoured after a visual appraisal of the differences between treatments, which data are plotted in Fig.3.9. This approach permitted a t-test of the expectation that the regression of FPO on muscle would have a greater slope value in the AL group than in the 1.2 group and, in turn, in the 1.2 group than in the 0.8 group. Fig.3.9 illustrates that the experimental outcomes were not significantly different ($p > 0.1$) from the expectations in either case.

P5: Gain of Gut Contents Furthermore, allometric analysis could not be justified in the testing of the expectation that the restricted lambs would have lower gut-fill than AL lambs, and so linear models of gut-fill regressed on muscle weight were again fitted for the purpose of testing for differences between treatments. The finding that 0.8 lambs (slope = 0.25, s.e. 0.01) had a significantly greater ($p < 0.05$) weight of gut-fill at a given degree of maturity that AL lambs (slope = 0.15, s.e. 0.17) went against expectations.

P6: Liveweight Gain The expected aggregate effect of the component differences was that AL lambs would gain LW faster than 1.2 lambs which, in turn, would gain LW faster than 0.8 lambs. Fig. 3.10 bears out that these differences were actually recorded. The 1.2 treatment groups are represented

[17] There was no effect of treatment on the yield of wool after washing; washed wool = 0.7 X unwashed wool.

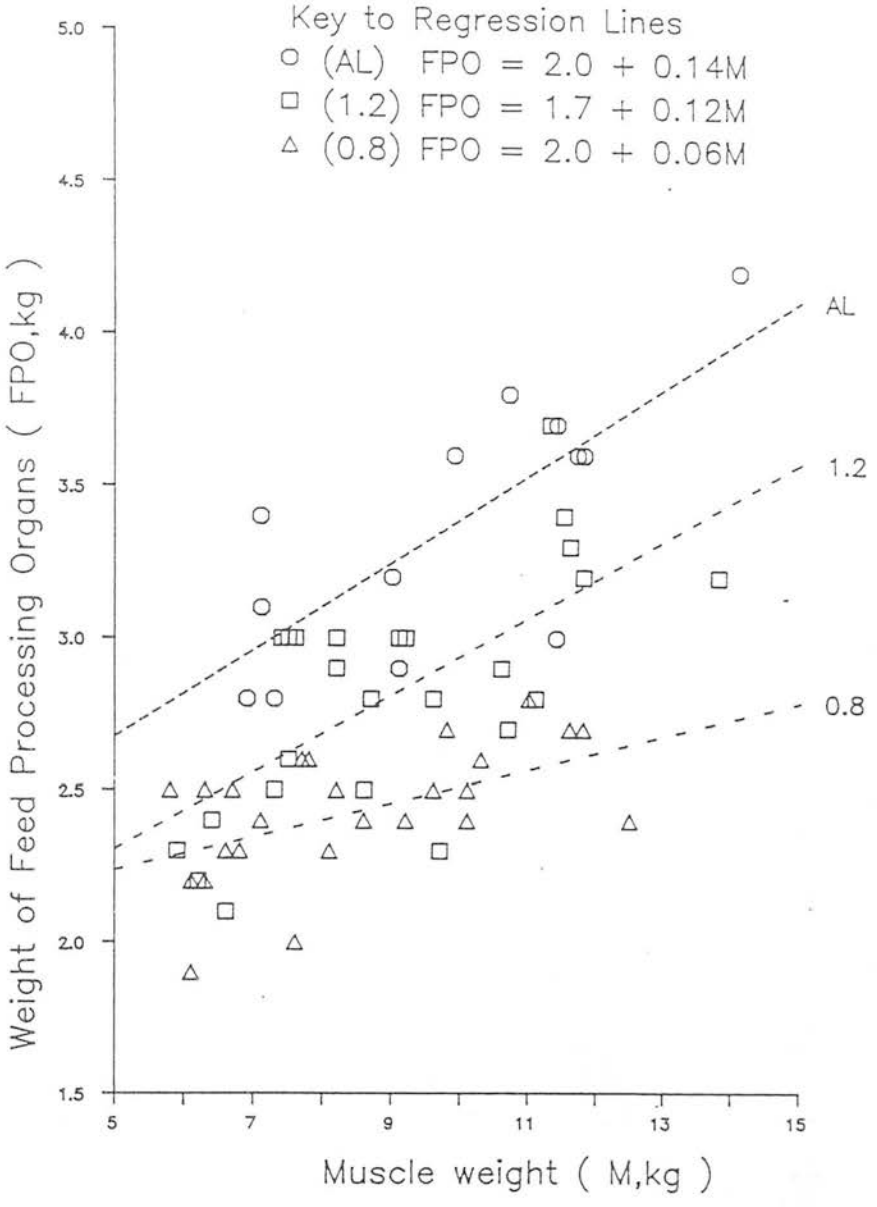


Fig. 3.9 The Effect of Feed Restrictions on the Relative Growth of the Feed Processing Organs (FPO) of Scottish Blackface Lambs

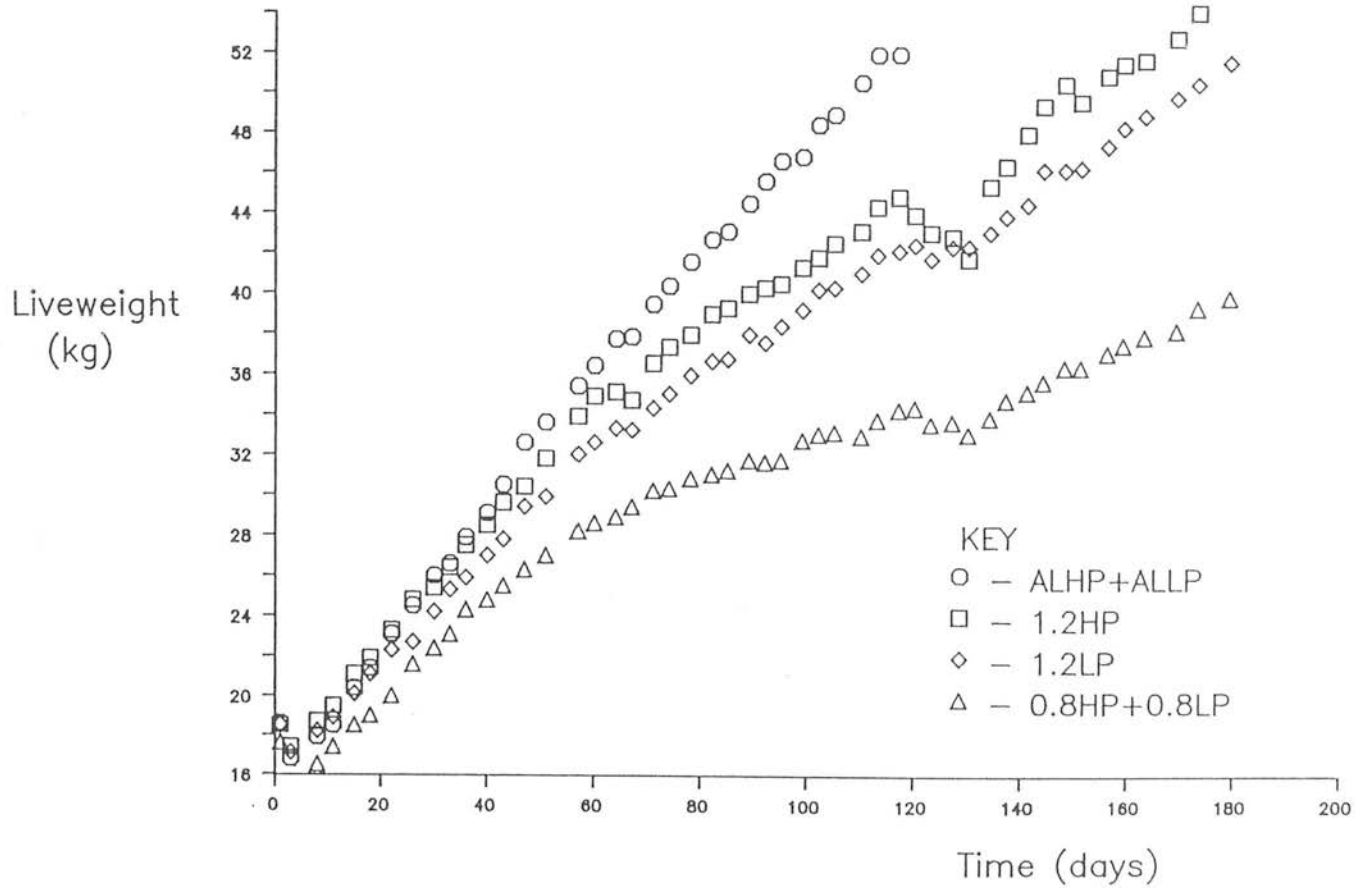


Fig. 3.10 The Liveweight Gain of Scottish Blackface wethers under Restricted Feeding Conditions

Table 3.7 Summary of the Analysis of Variance on the Proportions of Components in the Liveweight

Component	Significance of effect†		
	Liveweight	Treatment	Interaction
Head	***	***	**
Pelt	***	n.s.	n.s.
Feed-processing organs	***	***	n.s.
Gut-fill	***	***	n.s.
Muscle	***	*	*
Carcase fat	***	***	*
Carcase	***	**	*
Muscle and bone in the carcase	***	***	n.s.
Subcutaneous fat in the carcase	***	**	n.s.

† ***, $p<0.001$; **, $p<0.01$; *, $p<0.05$; n.s., $p>0.1$

separately because of the systematic differences in LW gain resulting from the reported and unexpected differences in rates of protein and lipid gain.

When the effects of treatment were viewed in terms of the changing proportions of component in the LW, some of the previously recorded differences were highlighted and others shadowed by this direct, but complex form of analysis (Table 3.7). For instance, treatment differences in the proportion of FPO ($p < 0.001$), gut-fill ($p < 0.001$) and head ($p < 0.001$) were recorded, but the differences in proportion of pelt disappeared ($p > 0.1$). The composite effects of treatment on the proportion of carcase were significant ($p < 0.01$) largely as a consequence of differences in degree of fatness which were highly significant when calculated as a proportion in the LW ($p < 0.001$) or in the carcase ($p < 0.01$). There were several significant interactions indicating that the treatments were responding differently in their proportions as LW increased.

Feed Conversion Ratio (FCR) The FCR (g feed intake/gLW gain), calculated for the first 20kg gain,was not significantly different ($p > 0.25$) between the ALHP lambs (4.0, s.e. 0.4) and the ALLP lambs (4.2, s.e. 0.4). In line with the recorded differences in lipid gain, the 1.2HP lambs used less feed for the same gain (FCR = 3.8, s.e. 0.5) but this difference was not significant ($p > 0.1$). The expected differences in FCR for the 1.2LP and 0.8HP treatments could no longer be justified because of the failure of these lambs to attain their potential protein growth rate. Consequently, 1.2LP lambs had an FCR of 4.6 (s.e. 0.2) which was significantly higher ($p < 0.05$) than that of the 1.2 HP lambs. 0.8HP lambs had an FCR of 5.7 (s.e. 0.3) which was significantly higher than that of 1.2HP lambs ($p < 0.001$) but was not significantly different ($p > 0.1$) from that of 0.8LP lambs (FCR = 6.3, s.e. 0.5).

3.5.5 Discussion

The several failures of the theory to predict the actual outcomes of the experiment obliged a review of the reasoning behind those predictions and a discussion of the methods and measurements carried out. Four main areas of disagreement were considered.

(i) *The 1.2LP and 0.8HP lambs failed to grow at their potential rate.* Criticism was directed, in this instance, at the formulation and level of

allowance of the feeds since the ALHP, 1.2HP and ALLP treatments had been shown to achieve the potential rate of growth.

(a) The two feeds had been formulated in the belief that, despite the restricted levels of feeding, their crude protein content, derived largely from soya bean meal, would have supplied sufficient protein to support potential growth. Since the 1.2HP CP allowance had been adequate, it could be concluded that a component of the protein became the first limiting resource in the 0.8HP, and to a lesser extent, the 1.2LP treatments and, therefore, that the model's assumption concerning nutrient: energy ratio of restricted allowances was not tenable in the ruminant. Alternative scales for measuring protein were mentioned in Chap. II, and the effect of feeding level on the protein supply was indicated in the review above. Since this experiment was designed specifically to ensure a similar CP allowance between treatments of different energy allowance, the outcomes would appear to support the idea that protein is less available to the ruminant at low levels of feeding.

On the assumption that a component of the protein was the first limiting nutrient, improvements in the design for future tests would include the use of a scale which recognises those protein sources known to be more available to the lamb, e.g. those which have a lower degradability (ARC, 1984) such as fishmeal. Problems could be encountered, however, in keeping energy allowances at comparable levels when using these scales. Finally, steps towards guaranteeing availability of vitamin and mineral resources could be made by regular injection of super-adequate quantities into the lambs.

(ii) *The 1.2HP lambs reduced their lipid: protein ratio* but the effect was not statistically significant despite lower rates of lipid gain than AL lambs. The problem here appeared to be two-fold.

(a) There were insufficient numbers of lambs on the treatment for the effect to acquire significance given the apparently high inherent variability in the fattening characteristics of the genotype. Unfortunately, resources had been allocated during the design of the experiment to the now unfulfilled 1.2LP and 0.8HP treatments.

(b) The allowance of 1.2kg did not impinge on the energy requirements for fattening in these lambs until a LW of c.22kg (see Fig. 3.6) and represented a super-maintenance allowance for the lambs at maturity, in which case, the

lambs would never have come to a fat-free immature equilibrium. They became relatively less restricted as they grew past the degree of maturity of maximum desired feed intake (c.42kg from Fig. 3.6).

It is recommended that future tests retain high protein allowances whilst decreasing the energy allowance below that of the 1.2HP treatment. Lloyd *et al* (1985) reported a more extreme effect on lipid: protein ratio by feeding 1kg/day of a similar feed to lambs of a higher mature size for which the energy restriction was presumably more severe.

(iii) *The restricted lambs distorted the desired form of the FFEB* by gaining relatively more head and more pelt than the AL lambs. Such effects have been reported previously (Palsson and Verges, 1952), but were considered to be open to the criticism that unmeasured fatness in the animal could affect the allometric analysis and hence exaggerate the departure from normality. This criticism remains relevant in the context of the results in this experiment. The allometry of head on muscle could be confounded by the significantly lower lipid content of the 0.8 lambs. The exclusion of wool from the argument over the reason for the higher pelt: muscle ratio in the restricted lambs leaves the probable cause as differential fatness in the skin. It is suggested that these doubts would most easily be settled by separate chemical analysis of the components, a technique favoured by Moulton *et al* (1922 and Mitchell *et al* (1928).

(iv) *The restricted lambs had more gut-fill than AL lambs*, the cause of which lay in the differences in feeding behaviour between treatments, and the shortness of the spell between feeding time and time of slaughter. For example, the 0.8 lambs were in the habit of consuming their feed allowance within half an hour of receiving it at 800h. Consequently, when slaughtered 5 hours later, the majority of their gut contents were recently consumed feed and water. AL lambs, on the other hand, ate regularly throughout the day and would be expected to have a smaller proportion of less digested feeds in their stomachs at time of slaughter. It is possible that the expected outcome would have been recorded had slaughter been carried out before feeding, or the allowance offered in several portions throughout the day.

3.5.6 Conclusions

The opportunity was taken in the discussion to re-examine the Theory of Growth under Limiting Conditions. In the light of this enquiry, it may be concluded:

(i) that lambs, given an allowance of feed which is not first limiting in a nutrient,

(a) put priority on protein growth and hence grow protein at the rate of their potential.

(b) gain lipid at a rate determined by the energy yield of the allowance and energy requirements for maintenance and growth.

(c) may show a smaller increase in lipid: protein ratio than fully-fed counterparts.

(d) show a smaller increase in feed-processing organ: muscle ratio that fully fed counterparts.

(ii) that lambs, given an allowance which is first limiting in a nutrient,

(a) also give protein growth priority but grow protein at the fastest rate permitted by the supply of the first limiting nutrient.

(b) gain lipid at a rate determined by the energy yield of the allowance and the energy requirements for maintenance and the slower rate of protein growth.

(c) show a smaller increase in feed-processing organ: muscle ratio than fully-fed counterparts.

(d) may show a greater increase in pelt: muscle and head: muscle ratios.

CHAPTER 4
GROWTH AFTER THE RESTORATION OF NON-LIMITING CONDITIONS

4.1 Introduction (The Fourth Path to Maturity)

At the outset of his studies on 'The Capacity of Animals to Grow under Adverse Conditions', Waters concluded that

> an animal that is below the normal in size at a given age, through poor nourishment, apparently has the capacity, when liberally fed, to compensate for this loss in a measure at least, by an increased rate of gain (Waters, 1908).

which he regarded as one of the four ways by which an animal could attain maturity. This statement addressed the agriculturally important issue of the response of animals to the restoration of non-limiting conditions when they had previously been retarded by a feed restriction, that is, the response of animals to realimentation.[18]

Since most wild or extensively reared animals, including sheep, are commonly liable to a limitation in their feed supply, animal productionists have been interested in the nature of growth made by realimented animals, and whether the effects of retardation are permanent or recoupable. They required to know the effect of a period of restricted feeding on the subsequent performance of the animal, and the feed needed to support that response. Recent surveys have reported that 50 per cent of lowground lambs and 90 per cent of hill lambs are not finished off grass at weaning because of low growth rates (Speedy, 1980; Lloyd, 1983). Hence the problem of recovery growth remains relevant to the sheep industry today. Furthermore, cattle farmers are encouraged by the savings they can make on hard-won winter feeds if it can be shown that the animals, fed on restricted planes of nutrition in the winter, are not impaired in their spring performance at grass.

Consequently, research into the recovery growth of farm animals has been very popular but the variety of responses observed has supported a number of *ad hoc* and often inconsistent theories which only partially explain the

[18] In this review, realimentation will always be taken as the restoration of non-limiting conditions (Chap. II). The principles of the growth of animals under limiting conditions are found in Chap. III.

phenomenon. For example, the reviews of Wilson and Osbourn (1960), Allden (1970) and O'Donovan (1984) called attention to the widely held belief that animals 'compensate' for or 'catch up' the time 'lost', during a phase of restricted growth, by subsequently growing faster when realimented. Unfortunately, the definition of growth is not standardised between reports, but 'compensatory growth' has been recorded as accelerated liveweight gain as well as accelerated protein gain. Some workers take compensatory growth to be possible because basal metabolic rate has often been lower in animals after a period of underfeeding, in which case accelerated gain would be supported by more efficient feed conversion of a certain voluntary feed intake (Wilson and Osbourn, 1960). Two sources of doubt arise over this argument. Firstly, measurement of maintenance energy requirement as a function of liveweight is made difficult by the possible changes in liveweight composition under limiting conditions. Secondly, the review of Chap. II has provided both theoretical and empirical grounds on which to suppose that the animal's actual or 'voluntary' feed intake will change in relation to the desired feed intake of the first limiting resource. Others view compensatory growth as a phenomenon of the physiological age of the animal (that is, it is related to degree of maturity) rather than its chronological age (Winchester and Ellis, 1957), but this approach does not always account for recovery growth in terms of extra fat gain, which is held by many (e.g. Pomeroy, 1955) as the explanation of compensatory gain.

4.2 A Theory of the Growth and Feed Intake of Sheep after the Restoration of Non-limiting Conditions.

It is difficult to reconcile such a range of opinions when each observation depended on the particular theoretical context in which it was made. Consequently, the view is invited that the three central ideas which embraced the previous chapters, namely, that:

(i) the potential form of the animal and the maximun rate of change in form possible, are retained throughout the animal's life in its inheritance (potential growth, Chap.I);

(ii) potential growth becomes actual under non-limiting conditions (Chap.II);

(iii) only the form of the fat-free empty body is inviolate under limiting conditions (Chap.III);

may also prevail in the growth of realimented animals.

The purpose of this review is to use experimental evidence, where applicable, to test the theory of recovery growth which arises from the view of animals developed through the thesis. The theory predicts that a realimented animal, at a given degree of maturity will seek to:

(1) resume the rate of growth known to be its potential (Chap. I), where growth is defined as a harmonious maturation of form, best measured by an increase in skeletal dimensions or an increase in ash and protein weight.

(2) replenish, if necessary, its fat stores to the level set by its inheritance (desired lipid: protein ratio, Chap. I).

(3) increase its feed intake to satisfy the residing, and now released, impulse to grow (Chap. II). The necessary conditions and the nature of resource partition for the fulfillment of this growth impulse remain those outlined in Chap. II and Chap. III respectively. The concomittant effects of the increase in feed intake are that the animal will:

(4) restitute, if necessary, the capacity and weight of its feed processing organs to the size set by its growth-plan. (Chap.I).

(5) increase its weight of gut contents.

4.2.1 The Retention of the Potential for Growth

The Missouri workers first subject in their study of the ability of animals to recover from a period of poor feeding was Steer 529 (Moulton *et al*, 1921). This individual was reportedly held at a liveweight of 200 pounds and a height at the withers of 96 centimetres for thirteen months before it was permitted to eat its feed *ad libitum*. The plot of the height at the withers of Steer 529 is shown in Fig. 4.1 compared with the average curve of its continuously, *ad libitum* fed counterparts. The growth check and subsequent recovery of Steer 529 can be seen clearly.

Steer 529 resumed growth at a rate expected for and comparable with that of other steers of similar kind and size, irrespective of age. In other words, growth rate, after the restoration of non-limiting conditions, remained dependent on the state of the animal (its degree of maturity) and the direction of its impulse for growth (Chap. I). This part of the theory resembles the opinions, typified by the conclusions of Winchester and Ellis (1957) which regard compensatory growth as a function of physiological age.

In those papers where the data are reported in a form which permits analysis of this kind to be carried out, there was also no clear indication that realimented pigs or sheep could better the growth rate of non-limited contemporaries at the same degree of maturity (McMeekan, 1940; Palsson and Verges, 1952). However, several workers have published data which show an accelerated protein gain in, for example, realimented sheep [Reid *et al*, 1968; Keenan, McManus and Freer (1969); McManus, *et al* (1972); Burton, Anderson and Reid (1974); Little and Sandland (1975); Drew and Reid (1975); Thornton, *et al* (1979); Tullis (1982)].

Unfortunately, the gain of protein in the feed processing organs was only measured separately from the gain of protein in the carcase in the work of Tullis (1982), and hence there are considered to be insufficient grounds on which to support the idea that the realimented animals truly grew faster than continuously-fed animals. This point will be elaborated in Section 4.2.4 of this review.

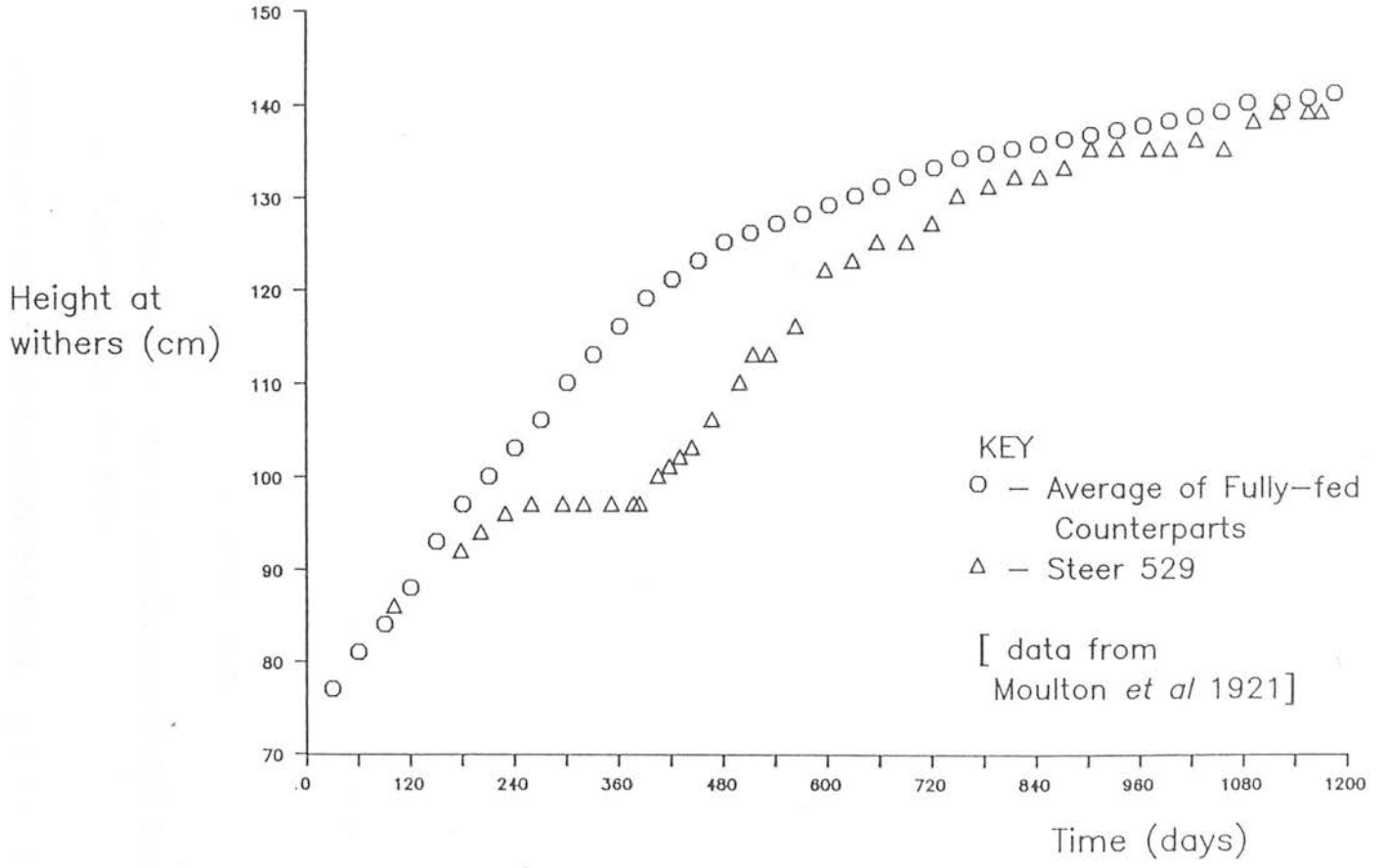


Fig. 4.1 The Growth of the Skeleton of Steer 529 following a period of underfeeding

4.2.2 The Restoration of the Desired Fatness

The idea that an animal inherits the tendency to seek a certain level of fatness was introduced in Chap. I.The theory posited that, under non-limiting conditions, the gain of lipid by the animal is related in a definite way to the growth of protein. The animal will only deviate from its desired lipid: protein ratio when obliged to under limiting, that is, under contrained (Chap. II) or restricted (Chap. III) feed conditions.

It is now asserted that the animal retains the desire for a certain lipid: protein ratio after realimentation, and hence, the subsequent rate of lipid gain of the realimented animal is seen to be dependent on the fatness of the animal after the feed restriction has ended. The rate of lipid gain, relative to that of continuously-fed counterparts, at the same degree of maturity, will be:

a) *faster* when the net effect of the restriction is a lower lipid: protein ratio than that desired.

b) *similar* when the restriction does not change the degree of fatness.

c) *slower* when the restriction produces an animal with a higher lipid: protein ratio than that desired.

In an analogous way to section 4.2.1, the rate of fattening is found to be dependent on the state of the animal (its degree of maturity and degree of fatness) and the direction of its impulse to fatten (Chap. I). This part of the theory relates to those workers who believed that compensatory gain was entirely attributable to extra fat gain (e.g. Pomeroy, 1955). When the literature is approached under the guidance of these principles, evidence may be found to support each of the three cases:

a) Lipid gain faster than continuously fed sheep

Wilson and Osborne (1960); Meyer and Clawson (1964); Searle and Graham (1975); Lawlor, Carroll and Poole (1976).

b) Lipid gain similar to continuously fed sheep.

Searle, Graham and Smith (1979); Thornton, *et al* (1979).

c) Lipid gains lower than continuously fed sheep

Reid, *et al* (1968);Keenan, *et al* (1969); McManus, *et al* (1972); Drew and Reid (1975); Little and Sandland (1975); Butler-Hogg (1984).

Such a view offers a reply to the authors Thornton, *et al* (1979) who wrote:

> Literature reports on the body composition of sheep which have undergone compensatory growth cover a spectrum from increased fat...deposition...through to unchanged, to less fat deposition...relative to continuously grown controls. *These findings cannot be reconciled and possibly represent the true spectrum of findings* which can result from separate experiments on limited numbers of animals with highly variable body compositions under a variety of conditions of nutritional restriction and realimentation.

4.2.3 The Increase in Feed Intake

When the animal is permitted to take feed *ad libitum* after a period of restriction, it is held that the feed resources required by the animal are to be allocated by the same partitioning rules given in Chaps. II and III, namely, for (i) maintenance, (ii) protein growth and (iii) lipid gain.

The contribution of the requirement for maintenance (preferably measured in relation to protein weight of the animal) and growth to the demand for feed will be, in accordance with section 4.2.1 above, the same for realimented and continuously-fed animals, but will be higher, the same or lower for lipid gain in relation to the energy required for the responses outlined in section 4.2.2.

The subject of feed intake after realimentation becomes more comprehensible when the factors which affect it are ordered in this manner and thus the findings in the literature may be analysed with more confidence.

The common observation that realimented sheep eat at a higher rate than continuously grown sheep is well documented [Allden, 1968; McManus *et al*, 1972; Graham and Searle, 1975; Graham and Searle, 1979]. The view is invited that the feed intake of realimented animals exceeds or equals that of continuously grown animals in accordance with the state of the animal (its degree of maturity and of fatness) and the direction of its impulse for growth and fattening after restriction, and that the feed intake and feed conversion

ratios of realimented lambs are entirely explicable in these terms. It is also considered that there will be occasions when feed intake is lower for realimented animals, at the same degree of maturity, in compliance with Rule 4.2.2. (c) above. For instance, Graham (1969) recorded that fat sheep ate less than unrestricted controls at the same degree of maturity. The shortage of data on this topic is probably a reflection of the difficulty in obtaining an animal which is appreciably fatter, than it desires to be, after a feed restriction (See Chap. III).

4.2.4 The Constriction of the Feed-processing Organs

The literature furnishes ample evidence to support the idea that realimented animals restitute their feed process in organs, in response to the increase load of feed, when necessary (Lawrence and Pearce, 1964; Peters, 1967; Keenan, *et al*, 1969; Winter, *et al*, 1976; Thornton *et al*, 1979).

Furthermore, it is contended here that those authors who observed faster protein gains in realimented animals (section 4.2.1) were, in fact, recording a similar restitution of the organs and not any acceleration in true growth. There are adequate reasons for suspecting this. Thornton *et al* (1979) openly attributed the extra gain in protein to a gain in organ protein. Moreover, Keenan, *et al* (1969), Butler Hogg (1984), Drew and Reid (1975) Burton *et al* (1974) reported increased water gain in addition to the extra protein gain in their experiments. It is suggested that this was probably an effect of rehydration of the gut tissues. Tullis (1982) assigned the accelerated nitrogen retention of her realimented pigs to repletion of labile nitrogen reserves.

4.2.5 The Increase in Gut Contents

Under conditions of restricted feeding sheep and other animals are expected and known to have lower weights of gut contents than fully-fed animals [Mitchell *et al* (1928); Burton *et al* (1974); Murray and Slezaceck, (1976)]. Concurrent with the increase in feed intake after realimentation, the weight of gut contents is therefore expected to rise, and for a time, exceed that of continuously fed animals until feed intake rate is equal in the two. Such were the findings of Burton *et al* (1974), Winter *et al* (1976), Searle *et al* (1979) and Thornton *et al* (1979).

4.2.6 The Response in Liveweight Gain

The four-component theory of the growth of realimented lambs may now be brought to bear on the problem of predicting the response of lambs in terms of their liveweight gain. That an understanding of the internal changes in the animal is necessary for such an understanding has already been called for many times (O'Donovan, 1984). The theory presented in this review has shown that the task of predicting liveweight responses is only achieveable when the following information about the animal, and its previous restriction, are available:

1) the animal type and its potential for growth (Chap. I)

2) the conditions for realimentation (non-limiting, Chap. II)

3) the degree of maturity of the animal (P_t/P_m)

4) the degree of fatness (lipid: protein ratio, Chap. III)

5) the weight of the guts (Chap. III)

6) the weight of gut contents (Chap. III)

Wilson and Osbourn (1960) made a similar note of the 'factors influencing an animal's ability to recover from the effects of undernutrition' which indicated a path through the conflicting opinions based on liveweight observation. Such opinions implied that the animal 'catches up' or 'compensates' for the time lost during the restriction because realimented animals make gains in liveweight at an accelerated rate compared with continuously fed animals. The liveweight data of Steer 529 could be used to support such a view (Fig. 4.2). But when it is also known, from the reported data, that the feed intake of Steer 529 increased faster than fully-fed controls (presumably for the restoration of fat depots); that feed-processing organs and gut contents will increase accordingly; and that the skeleton of Steer 529 did not grow any faster than the controls, any belief in true compensatory growth must be shaken. It is not denied that some benefits may accrue to the farmer who 'stores' his animals in winter on low planes of nutrition. He has the opportunity to vary the degree of fatness in his animals and can feed less of the more expensive winter feeds in the knowledge that the animals can continue to grow in the spring when feed

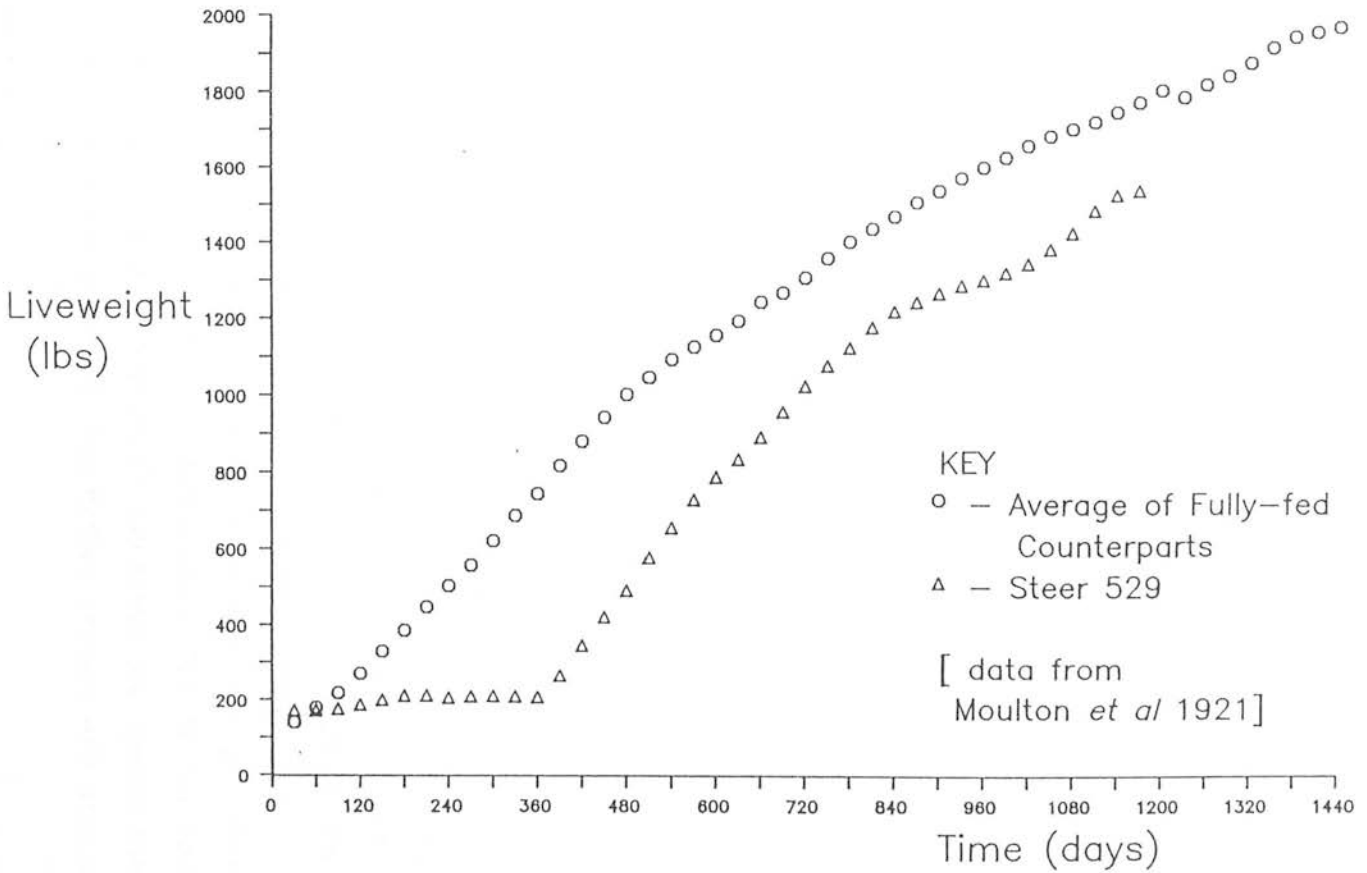


Fig. 4.2. The Path of Liveweight Recovery of Steer 529 following a period of underfeeding.

is more freely available. But, after taking into account all the factors mentioned, there is a striking lack of evidence to uphold the idea that muscle protein growth rate (which is one of the more reliable indicators of growth) is accelerated after realimentation.

4.2.7 Instances of Failure to Recover

The earliest investigators of the response of animals to full-feeding after a period of under-feeding were as aware of the possibility that the animal may fail to recover as they were that it may 'compensate'. Hence Osborne and Mendel (1914) felt justified in making the conclusion:

> It has been shown that the capacity to grow can be retained and exercised at periods far beyond the age at which growth ordinarily ceases. There seems to be no necessary impairment of the individual with respect to its ability subsequently to reach full size characteristic of the species [but] in prolonged stunting the animals may sometimes reach a precarious condition in which their vitality may be impaired beyond the possibility of recovery.

Thus, it may be said that animals recover, in the manner set forth in the previous review, on all occasions save after the most stringent restrictions, that is the Rules of Recovery Growth apply to growing animals on restricted but not sub-maintenance feeding (Chap. III). [19]

In those examples when individuals, which have not been severely restricted or starved, do not recover in the way predicted, the theory prompts investigation into the nature of the conditions for realimentation. The feeds must be non-limiting and therefore must comply with the requirements laid down in Chap. II. Wilson and Osbourn (1960) noted the influence that method of realimentation had on recovery growth. With regard to the ideal energy: protein ratio of the feed, this value may be shifted higher or lower during recovery, according to whether the animal is seeking to gain more or less lipid respectively than it would when continuously fed at the same degree of maturity. Osborne and Mendel (1915) expressed the opinion that, in order to compare properly the growth of realimented animals with continuously grown

[19] Work on the latter has been favoured by Australian workers (see Allden, 1970), particularly in conjunction with mature ewes, and in this instance, the rules of recovery from starvation may not agree totally with the theory described above.

counterparts, conditions must be non-limiting to both groups since:

> It should be noted that the resumption of growth has not been as perfect in every instance as the typical records have presented *A positive result in these cases is far more valuable than a failure*, because the latter may arise from a variety of extraneous, as well as inherent, causes which we cannot control or discover. Osborne and Mendel (1915)

4.3 Experiment 5. A Test of the Theory of Recovery Growth

4.3.1 Objectives

The potential for growth, the effect of feed restriction on body composition and the proposed general Theory of Recovery Growth were sufficiently well described to proceed with a further test of their usefulness in predicting the particular response of lambs, restricted in their growth rate from birth to 25kg liveweight, to the restoration of non-limiting conditions.

4.3.2 Propositions

For a prediction of the growth response of a given group of lambs to the restoration of non-limiting conditions, the following information, about the effect of feed restriction on the body composition of the lambs, should be available, viz:

a) the degree of fatness.

b) the weight of the guts.

c) the weight of the gut-contents.

The theory then generated a set of propositions, which hold that, upon realimentation:

P1: the lambs will resume muscle growth at the same rate as their unrestricted counterparts at comparable degrees of maturity. This rate of growth will be demonstrably that of their potential.

P2: the lambs will replenish, if necessary, their fat stores to the same fat: muscle ratio of their unrestricted counterparts. This fat: muscle ratio will be that set by their inheritance.

P3: the lambs will increase their rate of feed intake to satisfy the (a) residing and now released impulse to grow (muscle) and (b) replenishment, if necessary, of the fat reserves.

P4: the lambs will maintain the form of the fat-free empty body (excluding feed-processing organs) in accordance with their inheritance.

P5: the lambs will restitute, if necessary, the capacity and weight of their feed-processing organs (FPO) to accommodate the increased feed intake.

P6: the lambs will increase their weight of gut contents.

P7: the lambs may surpass the liveweight gain of their unrestricted counterparts, for a period, as a consequence of their extra gains in fat, gut and gut-fill components. Any differences in feed conversion ratio will be accounted for by differences in the composition of the liveweight gain.

4.3.3 Materials and Methods

Animals Two groups of male Scottish Blackface (SBF) lambs were selected on the basis of similar maternal treatment and similar birthweight [group 1 (n=20), 3.71 (s.d. 0.37)kg; group 2 (n=18), 3.87 (s.d. 0.36)kg; difference, n.s.] All the lambs were castrated within 24 hours of birth..

Feeds Each group of lambs was reared as one of a twin on ewes which were given access to a paddock consisting of a predominantly ryegrass sward. No supplementary feed was offered either to ewes or to lambs at grass. The composition and feeding value of the pelleted feed (F) offered to the weaned lambs is given in Tables 4.1 and 4.2. The feed was formulated to provide a non-limiting nutrient: energy ratio when offered to the lambs *ad libitum*.

Management The lambs were individually penned at weaning in a naturally ventilated earth-floored shed. Sawdust was provided as non-nutritious bedding. The lighting schedule was also fixed to give no less than 20 hours of light to the lambs. The LW of the lambs was recorded on five occasions (UR) and eight occasions (R), in the field, with a Poldenvale portable sheep weighing crate (100kg X 0.5kg). From 25kg LW, the lambs were weighed every Tuesday at 1300h. Feed was provided daily at 800h in kilogramme lots. Refusals were recorded thrice weekly on a Avery mechanical balance (15kg X 5g). The lambs were always given enough feed to ensure a refusal of 10-15%. Spillage losses could be estimated visually but were observed to be negligible.

Table 4.1 The Composition of the Pelleted Feed (g/kg freshweight) in Experiment 5

Ingredient	
Ground barley	390
Flaked maize	240
White fishmeal	67
Soya bean meal	86
Hay	143
Salt	19
Ground limestone	9
Nutrikem sheep trace element/vitamin mix	1
Molasses	45
	1000

Table 4.2 The Chemical Analysis and Feeding Value of the Pelleted Feed in Experiment 5

Constituent	g/kg freshweight
Crude protein (CP)	141
Crude fibre	73
Ash	67
Dry Matter	890
	per kg dry matter
Digestible organic matter (g)[a]	792
Digestible crude protein (g)[a]	134
Gross energy (MJ)	17.7
Digestible energy (MJ)[a]	14.7
Metabolisable energy (MJ)[a]	12.6

[a] *in vivo* measurements on 4 BF wethers offered feed *ad libitum*

Table 4.3 The Design of Experiment 5

Treatment	Period I Birth - 25 kg LW	Period II 25-45 kg LW	Serial slaughter programme Liveweight at slaughter	Number of lambs (per treatment)
R ('restricted')	(i) Ewes intensively stocked, sward height <3cm (ii) Lambs weaned at 18.2 kg LW, offered 700 g/day of feed F to 25 kg LW	Both treatment groups received *ad libitum* access to feed F	25 35 40 45	6 3 3 3
UR ('unrestricted')	(i) Ewes liberally stocked, sward height >5 cm (ii) Lambs weaned directly off ewes at 25 kg LW		Total	15

Design See Table 4.3.

(i) Birth - 25kg liveweight (LW)

Restriction in the growth of one group of the lambs from birth to 25kg LW was to be achieved by intensively stocking their ewes (M.Lloyd, personal communication) such that the sward height of their paddock never exceeded 3cm (Group 1 = treatment R, 'restricted'). However, the restriction was so severe and the condition of the ewes so depleted that the lambs had to be weaned before 25kg LW. They were housed at 96 (s.d. 7.5) days of age when they weighed 18.2 (s.d. 1.9)kg LW. The restricted rate of LW gain was maintained by offering the lambs an allowance of 700g/day of the pelleted feed.

The growth rate (and subsequent recovery) of the treatment R lambs was to be compared with that of well-fed counterparts (Group 2 = treatment UR, 'unrestricted'). The ewes of treatment UR lambs were liberally grazed such that the sward height of their paddock never fell below 5 cm. This treatment was intended to provide as high a plane of nutrition to the lambs as possible up to 25kgLW (M.Lloyd, personal communication).

(ii) 25 - 45kg LW

The recovery growth of the previously restricted (R) lambs was measured from 25 to 45kg LW. During this period, it was ensured that both groups of lambs were given non-limiting conditions for growth through the provision of *ad libitum* access to the pelleted feed.

Slaughter Schedule At birth, each lamb was assigned, at random, to one of four target slaughter LWs. The requirement for a firm estimate of the net effect of the feed restriction on body composition (in order to interpret the recovery phase) necessitated the slaughter of six lambs from each treatment at 25kg LW. Subsequently, a comparison of recovery growth with uninterrupted growth was made by slaughtering three lambs from each treatment at 35, 40, and 45kg LW. By this final LW, it was considered that all the effects of the feed restriction would have been overcome.

Slaughter and Physical Dissection Procedures When a lamb reached its target slaughter LW arrangements were made within three days for its slaughter at a commercial abattoir 30km distant. At 1500h on the day before slaughter, the lamb was weighed and transported to the abattoir. It was

provided with water and rested overnight. At 800h the following morning it was slaughtered by severance of the blood vessels in the neck. It was not possible to collect the draining blood but the following organs of the body were dissected and their weights recorded on a Salter (15kg X 50g) spring balance:

--head
--liver (with gall)
--stomachs (with intestines and spleen)
--caul fat
--warm carcase (including kidney)
--pluck (lungs and heart)
--feet

The stomachs and intestines were split open and the undigested contents scraped away and discarded. Empty gut weight was recorded and gut-fill estimated by difference. The carcase was recovered for physical dissection and stored at 4°C for no longer than two days. The remaining components were discarded.

Dissection of the Cold Carcase The procedure of tisssue separation was identical to that described in Appendix E. The dissection provided measurements of muscle, bone, subcutaneous fat, intermuscular fat and kidney knob and channel (perirenal) fat tissues.

4.3.4 Results

(i) Period of Restriction: Birth--25kg LW

a) Liveweight Gain (LWG)

Reference to the unplanned changes in the design has already implied that the intended depression in lamb growth rate by treatment R was achieved. Fig. 4.3 shows that the R lambs took significantly more time ($p < 0.001$) to reach 25 kg LW than UR lambs. The rates of LWG of the two groups from birth were 147 s.d. 24g/day and 281 s.d 29g/day respectively. A comparison with the Gompertz description of LWG taken from Chap. 1 suggested that the UR treatment lambs had received close to non-limiting conditions up to 25kg LW (see Fig. 4.3).

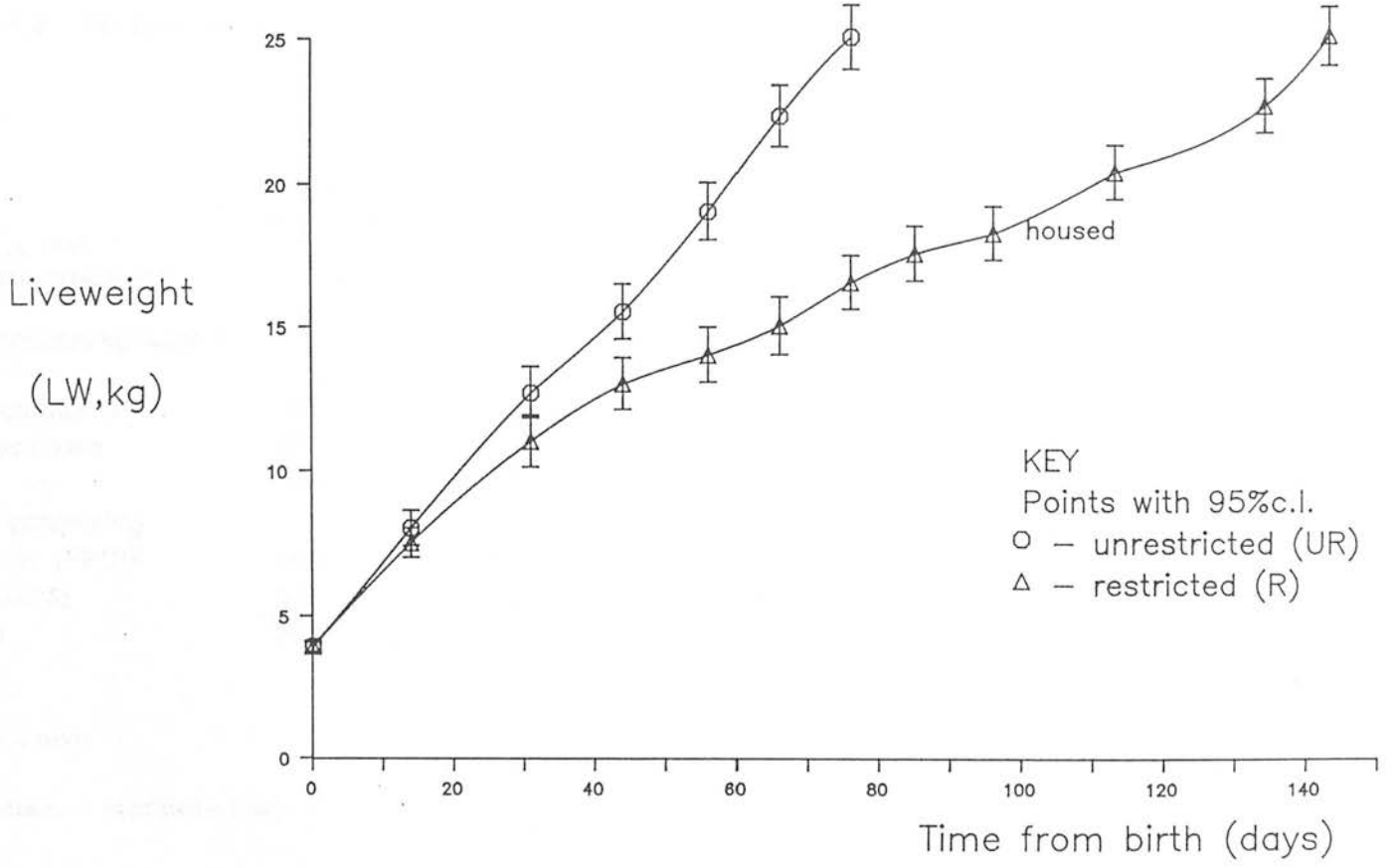


Fig. 4.3 The Effect of a Feed Restriction on the Liveweight Gain of Scottish Blackface wethers from birth to 25kg liveweight

Table 4.4 The Effect of a Feed Restriction on the Body Composition of Scottish Blackface wethers at 25 kg liveweight

	Unrestricted lambs (UR)	*s.e.*	Restricted lambs (R)	*s.e.*	Difference	Significance of difference
Carcase (kg)	10.78	0.32	9.11	0.34		
Carcase muscle (kg)	6.04	*0.22*	5.24	0.19	0.8	p<0.05
g component/kg muscle						
Total carcase fat	383	*30*	329	*38*	-54	n.s.
Carcase bone	326	*13*	338	*15*	12	n.s.
Pelt[a]	344	*16*	452	*15*	108	p<0.01
Feed-processing organs (FPO)[b]	404	*20*	437	*17*	33	n.s.
Gut-fill (GF)	596	*171*	896	*248*	300	p<0.05
Head	242	*17*	271	*19*	29	p<0.05

[a] (skin + wool)

[b] (stomachs + intestines + liver)

b) Body composition at 25kg LW

The effects of the feed restriction on body composition are described in Table 4.4 as component: muscle ratios. The table shows that UR and R lambs reached 25kg LW with significantly different ($p < 0.05$) weights of muscle (UR 6.0, s.e. 0.2kg; R 5.2, s.e. 0.2kg) but there was no indication that the restriction had caused R lambs to shift significantly ($p < 0.1$) from their desired fat, bone or feed-processing organs: muscle ratios. Consequently, in line with the theory, R lambs would not be expected to exhibit accelerated rates of gain in these components when realimented.

The less mature R lambs, however, had an unexpectedly and significantly higher ($p < 0.01$) pelt: muscle ratio at 25kg LW (452g pelt/kg muscle, s.e. 24) compared with UR lambs (344, s.e. 16). R lambs had a significantly higher ($p < 0.05$) head: muscle ratio (271, s.e. 8) than UR lambs (242, s.e. 7). Lastly, the higher gut-fill: muscle ratio of the less mature and more poorly-fed R lambs (896, s.e. 101) also differed significantly ($p < 0.05$) from that of the UR lambs (596, s.e. 70) in a manner contrary to expectations.

(ii) Period of Recovery: 25 - 45kg LW

P1: Muscle Growth Rate A similar procedure to that described in Exp. IV was used to organise the carcase muscle data into a suitable form for a convenient comparison of the derived Gompertz rate parameter, B value, with the expected value of 0.0081.

Initial muscle weight for each treatment was taken as the average from the initial slaughter group. Consequently, taking a mature muscle weight of 16.5kg, values for the B rate parameter for muscle gain could be calculated by transforming the estimated initial and known final muscle weights, divided by the known time to slaughter.

The value obtained for UR lambs was 0.0086 (s.e. 0.0003) which was not significantly different ($p > 0.25$) from either the expected value of 0.0081 (s.e. 0.0002) from Chap.I or from the value measured in Exp. 4 (0.0082, s.e. 0.0005). R lambs had a higher and more variable estimated B value for muscle gain (0.0099, s.e. 0.0007), which was not significantly different ($p > 0.1$) from the value for UR lambs.

P2: Relative Rate of Fattening The natural logarithms of both muscle and total carcase fat weights for each of the slaughtered lambs were plotted on the

same graph as the expected allometric relationship derived in section 1.1.1 for lambs fattening at their desired rate (Fig. 4.4).

The plots and regressions of the UR and R data declare that there were no significant differences in either slope (UR = 2.38, s.e. 0.22; R = 2.60, s.e. 0.24; difference, n.s., $p > 0.1$) or constant ($p > 0.1$) of the relative rates of fattening compared with the expectation, though a non-significant trend in the R lambs to become fatter than UR lambs at higher degrees of maturity is shown in Fig. 4.4. No significant differences ($p > 0.1$) were found between treatments in the relative rates of fattening in each of the fat depots in the body.

P3: Feed Intake The average daily feed intakes for both treatments from 25kg LW are presented in Fig. 4.5. The expectation that the previously restricted lambs would increase their rate of feed intake was fulfilled by the marked rise in feed intake of the R lambs from the level of the restricted allowances of 700g/day.

However, the body composition data of the R lambs at 25kg LW had revealed that the R lambs were less mature and would not require to replenish their fat reserves. In this case, the significantly greater rate of feed intake of the R lambs (1.34 s.d 0.15 kg/day) in the first three weeks of realimentation, compared with that of the UR lambs (1.06 s.d 0.18kg/day) went against the expectations of proposition (P3). There were no significant differences in rate of feed intake from three weeks onwards, but Fig. 4.5 indicates that, after eight weeks onwards, R lambs consistently ate less than UR lambs.

P4: The Form of the Fat-Free Empty Body The allometric relationship between bone and muscle (b values, UR = 0.76, s.e. 0.09; R = 0.72, s.e. 0.10) and head and muscle (b values, UR = 0.78, s.e. 0.07; R = 0.77, s.e. 0.07) did not disclose any significant ($p > 0.1$) or systematic deviations from the expectation of linearity. The pelt: muscle ratio, however, which was significantly different at 25kg LW, continued to be higher during the recovery period for R lambs (see Fig. 4.6), and the difference between treatments in the slope of the allometric regressions (UR = 1.45, s.e. 0.15; R = 1.12, s.e. 0.12) was highly significant ($p < 0.01$).

P5: Gain of Feed Processing Organs (FPO) Since the expected differences in FPO: muscle ratio was not apparent at 25kg LW, the expectation arising from proposition (P5) was that the relative growth rates of the FPO component

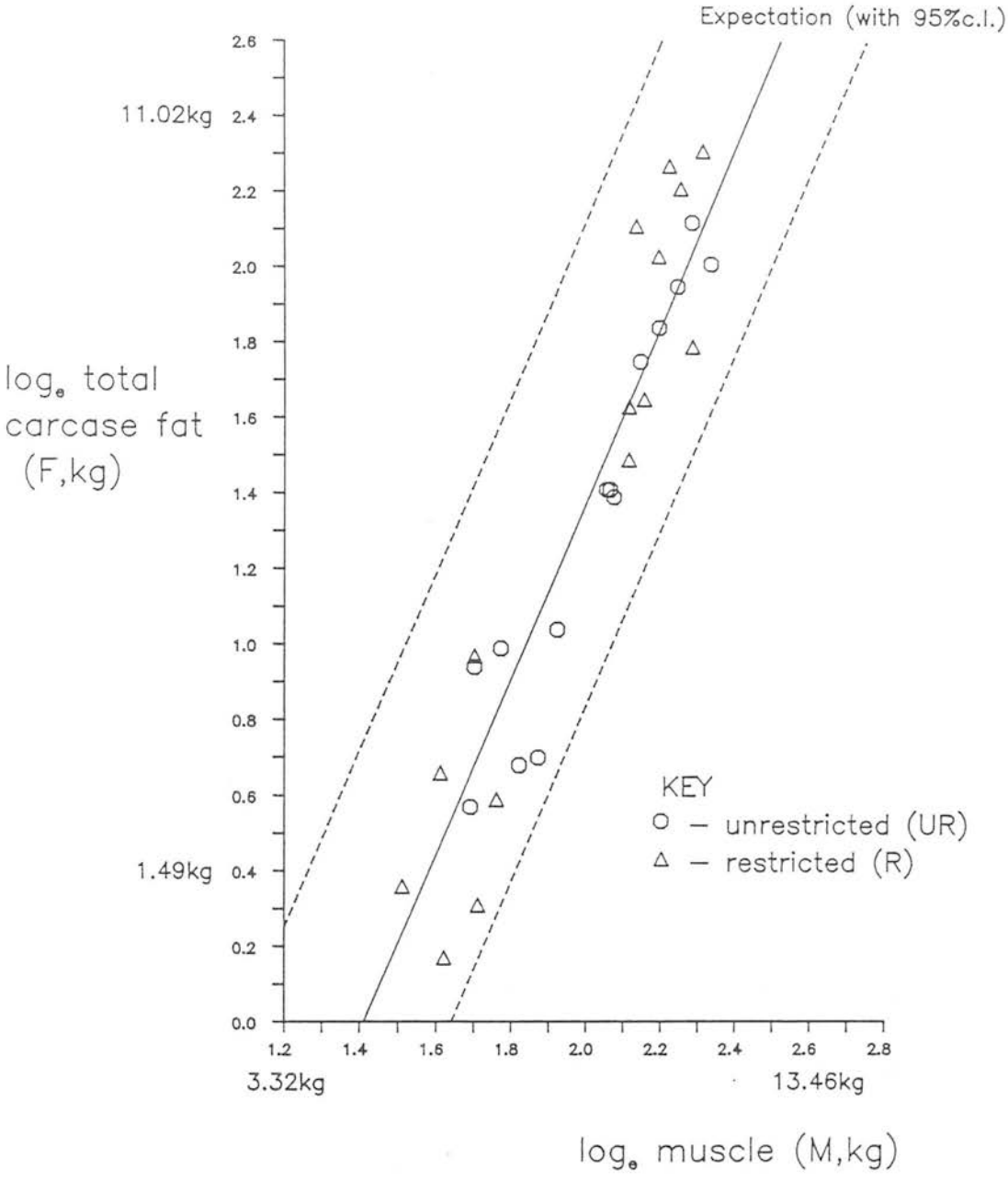


Fig. 4.4 The Allometric Relationship between Carcase Fat and Muscle in Fully–fed and Realimented Scottish Blackface wethers

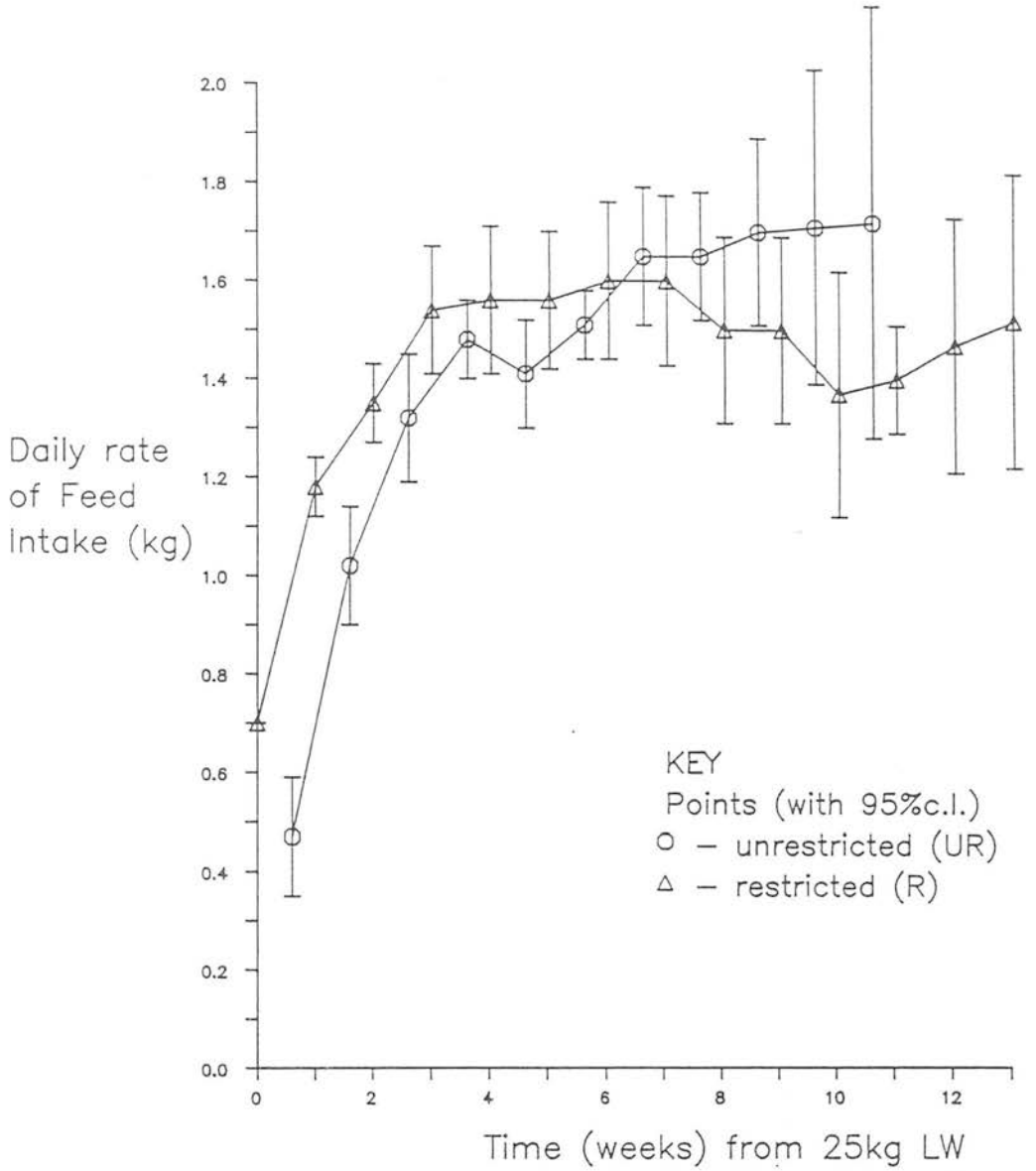


Fig. 4.5 The Rate of Feed Intake of Fully–fed and Realimented Scottish Blackface wethers

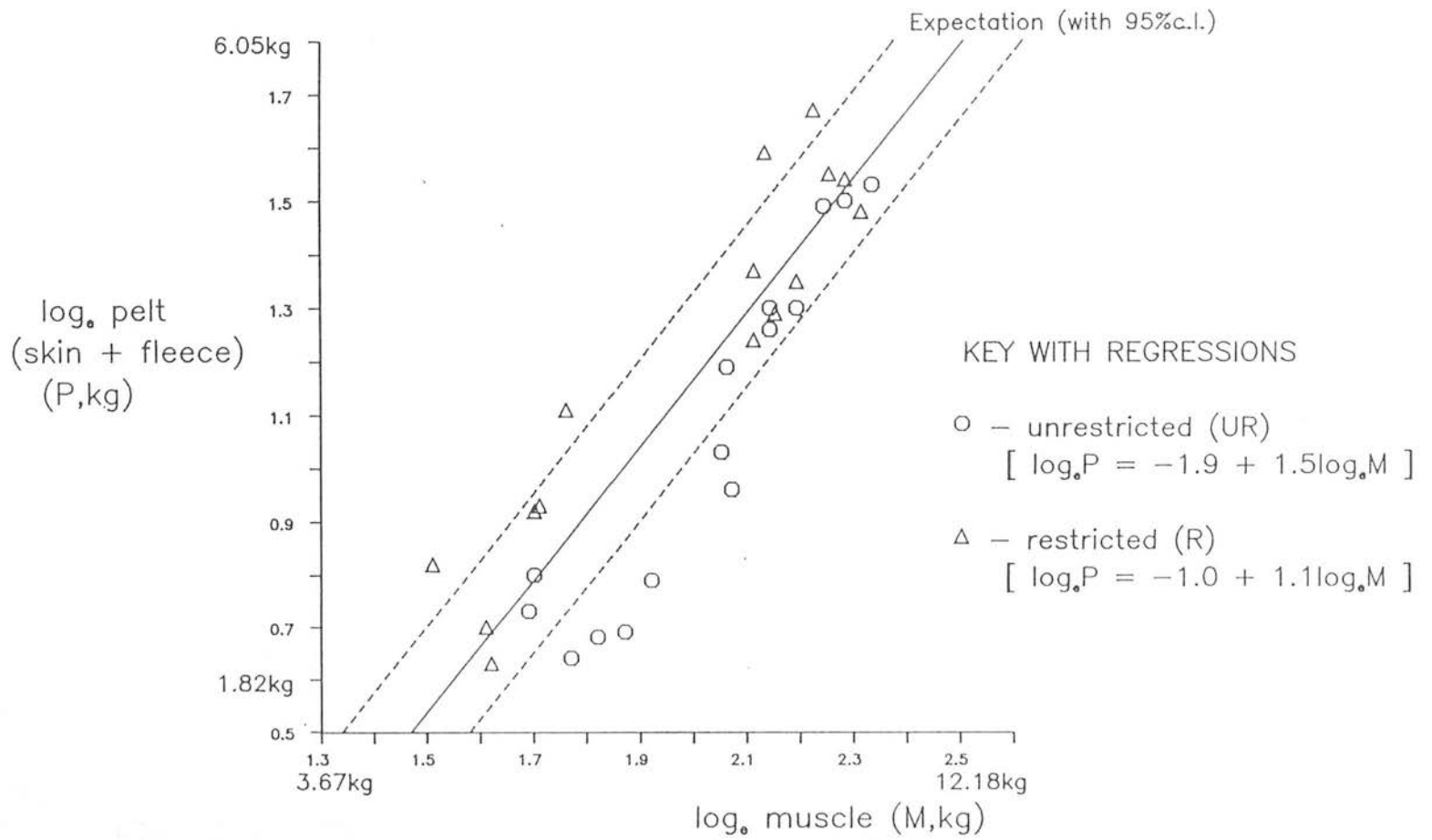


Fig. 4.6 The Allometric Relationship between Pelt and Muscle in Fully–fed and Realimented Scottish Blackface wethers

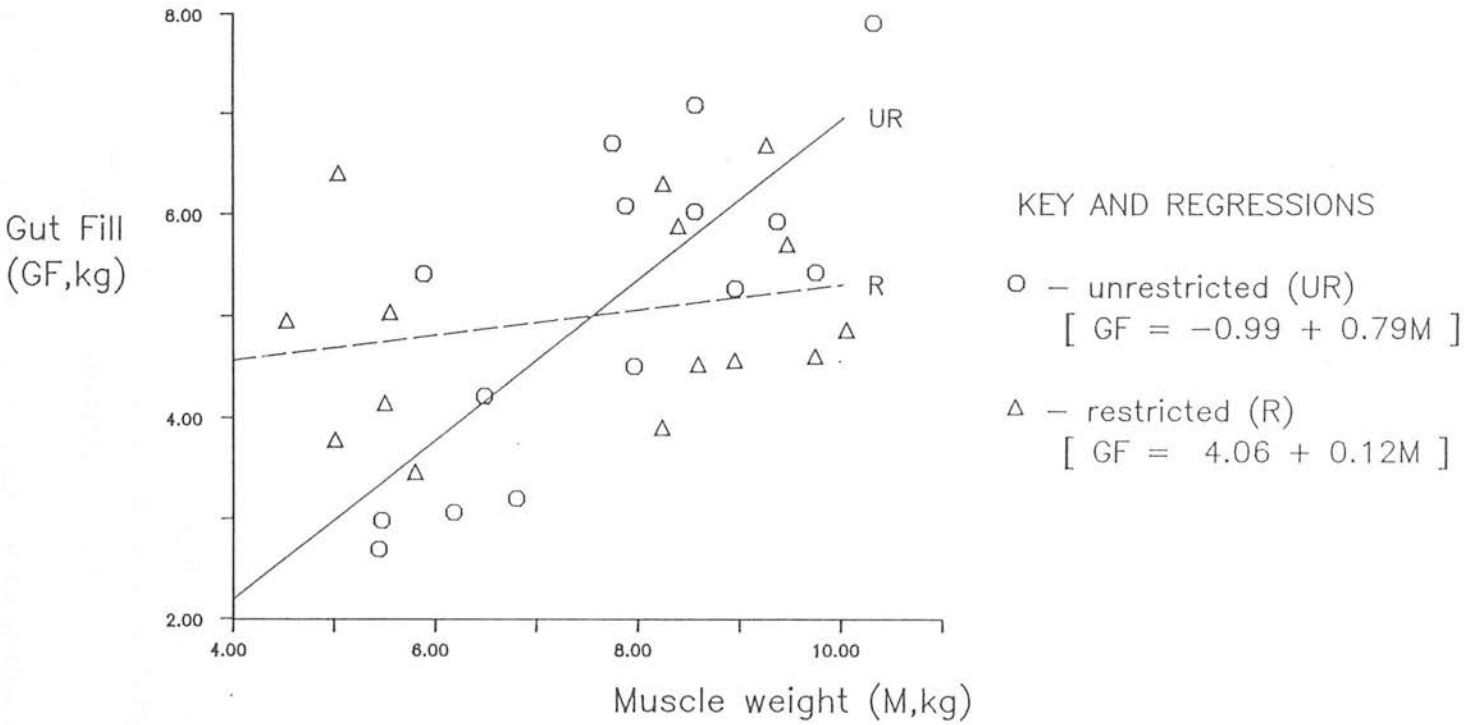


Fig. 4.7 The Relationship between Gut Fill and Muscle in Fully–fed and Realimented Scottish Blackface wethers

would be similar between both treatments from 25kg LW onwards. Neither the slopes (UR = 0.31, s.e. 0.07; R = 0.25,s.e. 0.07) nor the constants of the regressions of untransformed FPO on muscle differed significantly ($p > 0.1$) between treatments.

P6: Gain of Gut-Fill (GF) The high GF: muscle ratio in the R lambs at 25 kg LW also undermined the relevance of proposition (P6) that the recovering lambs would increase their weight of gut-fill. Fig. 4.7 demonstrates that the highly variable relationships between untransformed GF and muscle was of a different kind in R lambs than in UR lambs. UR lambs made substantial and significant ($p < 0.05$) increases in their weight of gut-fill (slope = 0.79, s.e. 0.018); R lambs did not (slope = 0.12,s.e. 0.14).

P7: Liveweight Gain The combined effect of similar rates of muscle growth, similar relative gains of fat and feed-processing organs and slower relative gains of pelt and gut-fill produced significant differences between the treatments in the LWG curve from 25kg LW (see Fig. 4.8). UR lambs gained LW at a daily rate of 386 (s.d. 73)g in the first two weeks from 25kg LW, a rate which was significantly greater ($p < 0.01$) that that of R lambs at 211 (s.d 92)g. Thereafter, the rates of LWG were parallel and not significantly different ($p > 0.1$) between treatments.

The overall effect that the series of differential component growth rates, which make up the LW curve, had on the proportions of each component in the LW were then subjected to an analysis of variance for the purpose of summarising the results (Table 4.5). The proportions of carcase and subcutaneous fat in the carcase were seen to rise significantly ($p < 0.001$) with increasing LW. The proportions of muscle and bone in the carcase, head and feed-processing organs fell. Treatment effects were only significant in proportion of pelt ($p < 0.001$) and head ($p < 0.05$) but the significant LW X treatment interactions in carcase proportion ($p < 0.001$) and gut-fill proportion ($p < 0.01$) indicate the influence that the initial body composition had on the subsequent development of the proportions in LW.

Finally, feed conversion ratio (FCR, g feed/ g gain) also differed significantly between treatments in accordance with the reported differences in feed intake and LWG. For example, in the first three weeks from 25kg LW, UR lambs (3.33,s.e. 0.24) had a significantly lower ($p < 0.01$) FCR than R lambs (6.09, s.e.

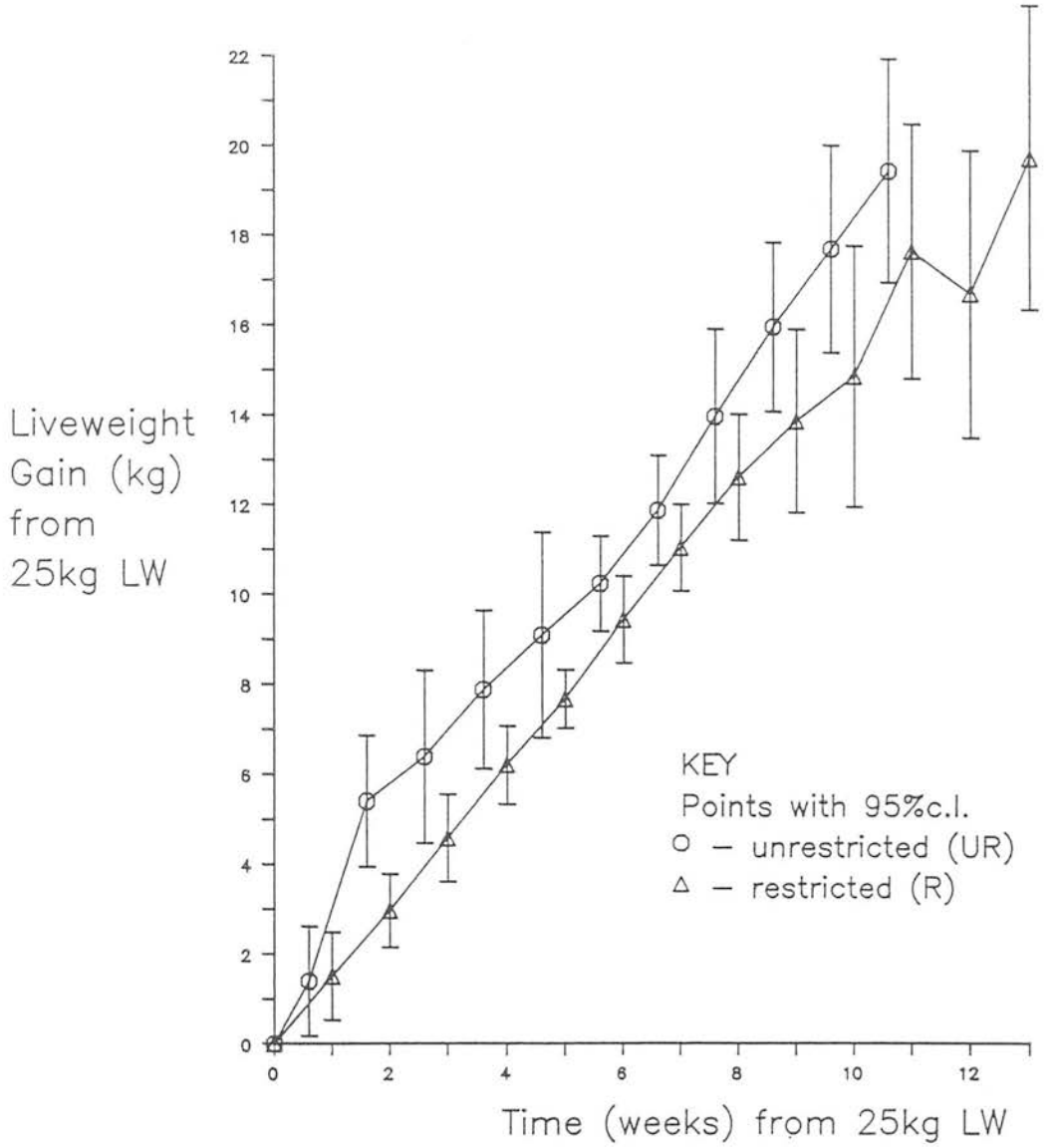


Fig. 4.8 The Path of Liveweight Recovery of Realimented Scottish Blackface wethers from 25kg liveweight

Table 4.5 Summary of the Analysis of Variance on the Proportions of Components in the Liveweight

	Significance of effect†		
Component	Liveweight	Treatment	Interaction
Head	***	*	*
Pelt	n.s.	***	n.s.
Feed-processing organs	*	n.s.	n.s.
Gut-fill	n.s.	n.s.	**
Carcase	***	n.s.	***
Muscle and bone in the carcase	***	n.s.	*
Subcutaneous fat in the carcase	***	n.s.	n.s.

† ***, $p<0.001$; **, $p<0.01$; *, $p<0.05$; n.s., $p>0.1$

0.35) Thereafter, the absence of differences in LWG and FI meant that FCR for UR lambs (5.84, s.e. 0.71) was not significantly different ($p > 0.1$) from that of R lambs (5.88, s.e. 0.39).

4.3.5 Discussion

The incidence of a number of disagreements between the expected outcomes of the experiment and those actually recorded has encouraged a reassessment of the theory in general and of the design of the experiment in particular. The following critique suggests three topics which contributed to these discrepancies.

(i) The emergency changes in design meant that R lambs received the pelleted feed F before 25kg LW. Consequently, the R lambs:

a) had a greater GF: muscle ratio than UR lambs at 25kg LW because the latter were presumably receiving a diet which consisted mostly of milk and any voluntary intake of grass.

b) made smaller gains in gut-fill than UR lambs from 25kg LW onwards (Fig. 4.7)

c) adapted more quickly to *ad libitum* feeding conditions and ate at a faster rate, than UR lambs from 25kg LW (Fig. 4.5)

d) gained LW more slowly and had a higher FCR (LW) from 25kg LW because gut-fill contributed less to their LW gain than it did in UR lambs.

e) showed significant interactions, but no difference from treatment UR, in the proportion of gut-fill (and hence proportion of cold carcase in the LW) between 25 and 45kg LW (Table 4.5).

With hindsight, the decision to wean the R lambs before 25kg LW proved unfortunate because it introduced such a large disparity between treatments in the above effects. A solution would have been to wean UR lambs before 25kg LW, and to offer them feed F *ad libitum* until they reached the 25kg LW. Initial body composition data and measurements of performance post-25kg LW could then have been made. This course of action was not available during the experiment because the growth of the UR lambs was too far advanced by the

time the decision was made to save the condition of the R ewes through the early weaning of their lambs.

The possibility of avoiding these problems by introducing differential nutrition through artificial rearing of the lambs had been considered, and had been attempted in another experiment. However, the data are not reported because the incidence of a 45% mortality rate forced the conclusion that neither the facilities nor the techniques used were of a sufficiently high standard to proceed with such work. Artificial rearing of lambs requires a high input of expertise and equipment, whereas the method of manipulating growth of lambs through maternal nutrition, has shown itself to be more reliable if adequate attention is paid to management techniques such as those suggested.

(ii) The theory failed to predict the net effect of the feed restriction on body composition. Consequently, R lambs:

a) were less mature than UR lambs, primarily as a result of higher gut-fill weight. This unexpected but explicable result did not obstruct the analysis of muscle growth rate but does emphasise the misleading nature of LW measurements for estimating degree of maturity in lambs.

b) had a greater FPO: muscle ratio than UR lambs. The problems of predicting the effects of feed quantity and type on the weight of the FPO fraction have recurred throughout this thesis. In this experiment, the effect may again reflect the unplanned provision of non-standardised feeding conditions before 25kg LW. It is suggested that more sensible data on the proliferation of gut components could be acquired be describing the feed offered more in relation to the activity required for its digestion (e.g. proportion of roughage) and by describing the severity of the allowance in relation to what the animal requires (i.e. feed intake under non-limiting conditions).

c) had a greater pelt: muscle ratio than UR lambs, though the effect was exaggerated by the unexpectedly low pelt: muscle ratio in the UR lambs at 25kgLW (see Fig. 4.6). Since the wool was not shorn off the lambs in this experiment, it was not possible to decide whether this effect resulted from higher wool weights in R lambs. However, the similar degree of fatness in the treatments would suggest that the differences in pelt weight were not due to differences in fatness, and hence weight, of the skin or muscle. The absence

of firm theories concerning the relation of wool growth to nutrition in growing lambs was mentioned in the review.

d) had a greater head: muscle ratio than UR lambs. This outcome agreed with the work of Palsson and Verges (1952) and the effect was also observed in Exp. 4. The strong rule that the form of the fat-free empty body is invariant may therefore have to be relaxed in this case. However, as was indicated previously, chemical analysis of each component would assist in determining the true extent of this effect.

(iii) The design allocated too few animals for estimating performance and body composition differences. Therefore, the anomalies, reported in the results cannot be given precedence in the conclusions because:

a) the R treatment B value for muscle gain showed a highly variable but non-significant tendency to be higher than that for UR lambs.

b) the systematic deviation in R treatment fat: muscle ratios at higher degrees of maturity were far from being statistically significant (Fig. 4.4).

c) feed intake and LWG data were being estimated from a decreasing mumber of lambs and recording had begun at different degrees of maturity.

If, as was the case in this experiment, the feed restriction did not shift body composition from the desired proportions set by the inheritance, the Theory of Recovery Growth predicted that there would be no differences in growth and feed intake between realimented and continuously grown animals from the same degree of maturity. The deficiencies in the design of this experiment listed above were encountered largely as a result of the unexpected similarity between treatments in body composition at 25kg LW after degree of maturity had been taken into account. A larger number of slaughtered lambs would be recommended for body composition analysis if the experiment were to be repeated. However, greater accuracy in feed intake and LWG estimate may be obtained, without large extra cost, by increasing the number of 'spare' test animals reared but not slaughtered.

4.3.6 Conclusions

The experimental tests of the Theory of Recovery Growth, and their elaboration in the discussion, have given sufficient grounds to conclude:

(i) that lambs, when realimented after a period of restricted feeding which does not alter their fat or feed-processing organ weight at a given degree of maturity

a) resume their muscle growth rate at the potential rate for their genotype.

b) continue to fatten in accordance with the characteristics of their inheritance.

c) maintain the form of the fat-free empty body (except pelt and head) as dictated by their inheritance.

d) eat a non-limiting feed at a rate which satisfies their energy requirement for maintenance, growth and fattening.

(ii) that LW is a poor indicator of the degree of maturity of a lamb and should not be used as the basis for a comparison of continuously grown and realimented lambs.

(iii) that lambs, during a period of under feeding, can increase their pelt: muscle and head: muscle ratios above that of continuously grown counterparts.

CONCLUDING REMARKS

In this thesis an attempt has been made to develop a general theory of the growth and feed intake of sheep. At each point in the argument, the data from experiments conducted under conditions which satisfy the requirements of the theory, have been compared with the expectations, and where data have been lacking, they have been obtained.

The interchange between theory and experiment has led to the formulation of an empirical description of the expected potential growth of the sheep (Chapter I) and the conditions under which it may be achieved (Chapter II). It is held that a description of the inheritance under these conditions is an important starting-point for both the scientist and the productionist, since it offers a standard by which the effects of a given treatment or feeding system may be judged.

The scientist may distinguish more accurately the contribution of the 'genotype' from that of the 'environment' in growth and may then be able to make more general statements about the former by the rules suggested in Chapter I. Furthermore, the preferred method of providing a non-limiting environment for the sheep, by giving it accces to more than one feed, has emerged as a useful tool for the nutritionist and the student of animal feeding behaviour. Given the choice between two feeds, one abundant in crude protein, the other deficient, the findings of Experiments 1 and 2 have shown that growing lambs can choose a non-limiting combination of the feeds which minimises excess protein intake. Since the theory regards such an outcome to be, by definition, a reflection of the lamb's needs, it is hoped that the opportunity will be taken to challenge further this idea in the future alongside more established methods for assessing nutrient requirements. In Experiment 3 ideas were tested concerning diet selection in lambs given feeds which differed in their bulkiness. Whilst lambs retained the ability to choose a non-limiting diet when given the chance, the undeveloped nature of the theory and the experimental designs which it generates offered a basis for future prediction of the feeding behaviour of sheep in the field, where the feeds available may all, for some part of the grazing season, be limiting in their bulkiness.

In turn, an understanding of feed intake and grazing behaviour becomes useful to the productionist who needs to predict the type and quantity of the

feeds used by his stock. Moreover, the description of the sheep's inherent capability to grow takes on a different value to the farmer who may wish to forecast the potential revenue from maximum output by his stock and then relate this output to the cost and effort of providing the necessary feeding conditions.

However, since in most farming situations the provision of non-limiting conditions for growth is not practicable, the farmer will more often be in the position of having to decide how much production is forsaken by rearing lambs at grass, that is, on a less nutritious feed which is cheaper and more extensively managed than its non-limiting alternatives. To solve this problem, the farmer needs a knowledge of what it is that is limiting the growth of his stock and what the responses of lambs to limiting conditions are. Chapter III was developed along a similar line of thinking. There, the view was taken that, in most cases, the form of the lipid-free empty body (excluding guts) was independent of feeding and that the most pronounced, and economically important, differences in growth occur as a result of the lamb's patitioning of the first limiting resource into protein and lipid gain. By this approach, manipulation of body and carcase fatness was shown to be possible in theory but confirmatory evidence was difficult to find. Experiment 4, however, supported the belief that lambs do partition a scarce energy resource to support protein gain before lipid gain but it was concluded that this effect is complicated in the ruminant because protein supply is not independent of feeding level.

The importance of future study into protein supply to growing lambs was therefore highlighted by these findings. Improvements in the design of restricted feeding experiments were suggested. One of the implications of the work to the sheep industry is that the fatness of lamb carcases can be decreased by nutritional means and that this may be one quick method of responding to the apparent demand for leaner mutton. However, given the nature of the ruminant and its importance other than as a meat yielder, there must remain practical difficulties in providing feed restrictions which are not first limiting in a nutrient under extensive farming conditions.

The views of the first three chapters were united in Chapter IV for the task of describing the recovery of lambs from a period of restrained growth. The theory that realimented lambs resume their known potential for growth and

then restore their body composition to the state dictated by their inheritance only when necessary, withstood tests with the available data and with Experiment 5. The existence of 'compensatory growth' was seen to depend on measurement of accelerated rates of gain in gut-fill, gut or fat (and hence liveweight gain), none of which are considered to be indicators of true progress to maturity. Consequently, stiffer methods for testing the proposed theory were recommended for the future. These suggestions included measurement of responses, particularly in the chemical components of the carcase, guts and pelt, in the first few days post-restriction. For a fair test of the lamb's ability to recover, however, non-limiting conditions must be provided along the guidelines given in Chapter II. In relation to lamb production, these findings suggest that the potential for non-limited growth remains with lambs which have suffered a growth check. However, it is important to recognise that such lambs are physiologically less mature than their chronological age might suggest and that they therefore require feeds of a nutrient: energy ratio appropriate to their degree of maturity if they are to achieve the growth rates of which they are capable.

APPENDIX A
BIBLIOGRAPHY

ALLDEN, W.G.(1968). Undernutrition of the Merino Sheep and its sequelae. *Aust. J. Agric. Res.* 19: 997-1007.

ALLDEN, W.G.(1968). The Effects of Nutritional Deprivation on the subsequent productivity of Sheep and Cattle. *Nutr. Abstr. Revs.* 40: 1167-1184.

ANDIK, I., DONHOFFER,S., FARKAS, M., AND SCHMIDT, P (1963). Ambient temperature and survival on a protein-deficient diet. *Brit. J. Nutr.* 17: 257-261.

ANDREWS, R.P. AND ORSKOV, E.R. (1970a). The nutrition of the early weaned lamb. I. The influence of protein concentration and feeding level on rate of gain in body weight. *J. Agric. Sci. Camb.* 75: 11-18.

ANDREWS, R.P. AND ORSKOV, E.R. (1970b). The nutrition of the early weaned lamb. II. The effect of dietary protein concentration, feeding level and sex on body composition at two liveweights. *J. Agric. Sci. Camb.* 75: 19-26.

ARISTOTLE. De Motu Animalium. With an English translation by E.S.Forster (1937) The Loeb Classical Library, Vol.XII, London: Heinemann.

ARC (1984). The Nutrient Requirements of Ruminant Livestock. Agricultural Research Council, Farnham Royal: Lavenham Press Ltd.

ARMSBY, H.P. (1908). The Principles of Animal Nutrition with special Reference to the Nutrition of Farm Animals. 3rd edition. New York: John Wiley & Sons.

ARMSBY, H.P. AND MOULTON, C.R. (1925). The animal as a converter of matter and energy, a study of the role of live stock in food production. New York: Chemical Catalog Co., Inc..

BAILE, C.A. AND PFANDER, W.H. (1967). Ration density as a factor controlling food intake in ruminants. *J. Dairy Sci.* 50: 77-80.

BALCH, C.C. and CAMPLING, R.C. (1962) Regulation of Voluntary Food Intake in Ruminants. *Nutr. Abst. Rev.* 32 (3): 669-686.

BANTA, L. (1932). What judgement does a hen use in selecting her food? *Poult. Sci.* II: 364.

BERG, R.T. AND BUTTERFIELD, R.M. (1976). New concepts of cattle growth. Sydney University Press.

BLACK, J.L. (1974) Manipulation of body composition through nutrition. *Proceedings of the Australian Society of Animal Production* 10: 211-218.

BLAIR, R. AND FITZSIMONS, J. (1970) A note on the voluntary feed intake and growth of pigs given diets containing an extremely bitter compound. *Anim. Prod.* 529-530.

Griffiths (1975) Black's earlier paper. Br. J. Nutr. 33, 399

BLAXTER, K.L. (1950). Energy feeding standards for dairy cattle. *Nutr. Abstr. Revs.* 20 (1): 1-21.

BLAXTER, K.L. (1962) The Energy Metabolism of Ruminants. London: Hutchinson.

BLAXTER, K.L., FOWLER, V.R. AND GILL, J.C. (1982). A study of the growth of sheep to maturity. *J. Agric. Sci. Camb.* 98: 405-420.

BOCCARD, R. AND DUPLAN, J.M. (1961) Etude de la Production de la Viande chez les ovins. III. Note sur l'influence de la vitesse de croissance sur la composition corporelle des agneaux. Annales de Zootechnie. 10: 31-38.

BONNIER, G. AND HANSSON, A. (1946) *Acta. Agric. Suecana*, 1: 171.

BRODY, S. (1945). Bioenergetics and Growth. New York: Reinhold.

BURTON, J.H., ANDERSON, M., AND REID, J.T. (1974). Some biological aspects of partial starvation. THe effect of weight loss and regrowth on body composition in sheep. *Br. J. Nutr.* 32: 515-527.

BURTON, J.H. AND REID, J.T. (1969). Interrelationships among energy input, body size, age and body composition in sheep. *J. Nutr.* 97: 517-524.

BUTLER-HOGG, B.W. (1984) Growth patterns in sheep: changes in the chemical composition of the empty body and its constituent parts during weight loss and compensatory growth. *J. Agric. Sci. Camb* 103: 17-24.

BUTLER-HOGG, B.W. AND TULLOH, H.M. (1982). Growth patterns in sheep: the effects of weight losses on compensatory growth and feed intake in Corriedale sheep. *J. Agric. Camb.* 99: 641-649.

BUTTERFIELD, R.M., GRIFFITHS, D.A., THOMPSON, J.M., ZAMORA, J. AND JAMES, A.M. (1983a). Changes in body composition relative to weight and maturity in large and small strains of Australian Merino rams.

1. Muscle, bone and fat. *Anim. Prod.* 36: 29-37.

2. Individual muscles and muscle groups *Anim.Prod.* 36: 165-174.

3. Body organs. *Anim.Prod.* 36: 461-470.

4. Fat depots and bones. *Anim.Prod.* 37: 423-431.

CAMERON, N.D. AND DRURY, D.J. (1985). Comparison of terminal sire breeds for growth and carcass traits in crossbred lambs. *Anim. Prod.* 40: 315-322.

CAMPLING, R.C. (1964). Factors affecting the voluntary intake of grass. *Prod. Nutr. Soc.* 23: 80-88.

CARREL, A. (1931). 'The new cytology' *Science* 73: 298, cited in Brody (1945), p.640.

CARTER, A.H. AND KIRTON, A.H. (1975). Lamb production performance of 14 sire breeds mated to New Zealand Rowney ewes. *Livest. Prod. Soc.* 2: 157-166.

CLARKE, M.L., HARVEY,D.G. AND HUMPHREYS, D.J. (1981) Veterinary Toxicology London: Balliere Tindall.

COCHRAN, W.G. AND COX, G.M. (1950). Experimental Designs. New York: John Wiley & Sons.

CONRAD, H.R., PRATT, A.D. AND HIBBS, J.W. (1964). Regulation of feed intake in dairy cows. 1. Change in importance of physical and physiological factors with increasing digestibility. *J. Dairy Sci.* 47: 54-62.

COPPOCK, C.E., EVERETT, R.W. AND MERRILL, W.G. (1972). Effect of ration on free choice consumption of calcium-phosphorous supplement by dairy cattle. *J. Dairy Sci.* 55: 245.

COURTIS, S.A. (1937) What is a growth cycle? *Growth* 1: 155-174.

COWAN, P.J. AND MICHIE, W.. (1977) Environmental temperature and choice feeding of the broiler. *Br. J. Nutr.* 40: 311-315.

CROSTON, D AND POLLOTT, G. (1985). Planned Sheep Production. London: Collins.

DAVIES, H.L. (1962). Intake studies in sheep involving high fluid intake. *Proc. Austl. Soc. Anim. Prod.* 4: 167-171.

DEVILAT, J., POND, W.G. AND MILLER. P.D. (1970). Dietary amino acid balance in growing-finishing pigs: the effect of diet preference and performance. *J. Anim. Sci.* 30: 536-543.

DINIUS, D.A. AND BAUMGARDT, B.R. (1970). Regulation of food intake in ruminants. 6. Influence of calorific density of pelleted rations. *J. Dairy Sci.* 53: 311-316.

DREW, K.R. and REID, J.T. (1975). Compensatory growth in immature sheep. I. The effects of weight loss and realimentation on the whole body composition. *J. Agric. Sci. Camb.* 85: 193-204.

DUFFUS, J.H. (1980). Environmental Toxicology. London: Arnold.

ECKLES, C.H. AND SWETT, W.W. (1918). Some factors influencing the rate of growth and the size of dairy heifers at maturity. *Univ. Miss. Agr. Exp. Sta. Res. Bull.* 31: 2-56.

EGAN, E.F. AND MOIR, R.J. (1964). Nutritional status and intake regulation in sheep. 1. Effects of duodenally infused single doses of casein, urea and propionate upon voluntary intake of low protein roughage. *Aus. J. Agric. Res.* 16: 437-449.

ELSLEY, F.W.H., McDONALD, I., AND FOWLER, V.R. (1964). The effect of plane of nutrition on the carcases of pigs and lambs when variations in fat content are excluded. *Anim. Prod.* 6: 141-154.

EMMANS, G.C. (1977). The nutrient intake of laying hens given a choice of diets, in relation to their production requirements. *Br. Poult. Sci.* 18: 227.

EMMANS, G.C. (1984). An additive and linear energy scale. *Anim. Prod.* 38: 538.

EMMANS, G.C. (1985). A general method to predict the unconstrained food intake of an immature animal. *Anim. Prod.* 40: 569.

EMMANS, G.C. (1986). A model of the food intake, growth and body composition of pigs fed *ad libitum*. *Anim. Prod.* 42: 471.

EMMANS, G.C. (1987). The predicted and actual rates of intake of a high quality food by Suffolk rams from 20 to 70kg liveweight. *Anim.Prod.* 44: 476.

EMMANS, G.C. (1988). The energy requirements of immature animals. [submitted to *J.Agric.Sci.Camb.*]

EMMANS, G.C. AND FISHER, C. (1986). Problems in nutritional theory, in *Nutrient requirements of poultry and nutrition research*, Chap.2, Poultry Symposium Number 19, edited by Fisher, C. and Boorman, K.N. Butterworths.

EVVARD, J.M. (1915). Is the appetite of swine a reliable indication of physiological needs? *Prod. Iowa Acad. Sci.* 22: 375-403.

FORBES, J.M. (1987) The voluntary food intake of farm animals. London: Butterworths.

FOWLER, V.R. (1968) Body develpoment and some problems of its evaluation. In *Growth and development of mammals*, Ed. Lodge, G.A. and Lamming, G.E. London: Butterworths.

FRASER, A.H.H. (1935). The influence of nutrition on wool growth. *Nutr. Abstr. Revs.* 4: 9-13.

FUNK, E.M. (1932). Can the chick balance its ration? *Poult. Sci.* 11: 94-97.

GIBB, M.J. AND PENNING, P.D. (1972). The effects of environmental temperature and feeding pattern on the performance of artificially-reared lambs fed cold milk substitute. *Anim. Prod.* 15: 177-182.

GLIMP, H.A. (1971). Effect of diet composition on diet preference by lambs. *J. Anim. Sci.* 33: 862-864.

GOMPERTZ, B. (1825). On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of Life Contingencies. *Phil. Trans. Roy. Soc.* 115: 513-585.

GORDON, J.G. AND TRIBE, D.E. (1951). The self selection of diet by pregnant ewes. *J. Agric. Sci. Camb.* 41: 187-190.

GOULD, S.J. AND LEWONTIN, R.C. (1979). The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. Soc. Lond.B* 205: 581-598.

GRAHAM, W.R. (1932). Can we learn anything from a free-choice of feeds as exressed by chicks? *Poult. Sci.* II: 365-366.

GRAHAM, N.M. AND SEARLE, T.W. (1979). Studies of weaned lambs before, during and after a period of weight loss. I. Energy and nitrogen utilisation. *Aust. J. Agric. Res.* 30: 513-523.

GRIFFITHS, W. AND HARMON, C. (1954). Self-selection of diets in wild and domesticated Norway rats. *Japan Psych. Res.* 19: 9-20.

GUNTHER, B. AND GUERRA, E. (1955). Biological similarities. *Acta Physiol. latinoam* 5: 169-186.

HAMMOND, J. (1921). On the relative growth and development of various breeds and crosses of sheep. *J. Agric. Sci. Camb.* 11: 367-407.

HAMMOND, J. (1932). Growth and development of Mutton Qualities in the Sheep; a survey of the problems involved in meat production. Edinburgh: Oliver and Boyd.

HARRIMAN, A. (1974) Self-selection of diet by Southern Plains wood rats *Neotoma micropus*. *J. Gen. Psych.* 70: 53-61.

HENRY, W.A. (1902). Feeds and Feeding: a hand-book for the student and stockman. 4th ed. Madison, Wis: W.A. Henry.

HODGE, R.W. (1974) Efficiency of food conversion and body composition of the preruminant lamb and the young pig. *Br. J. Nutr.* 32: 113-126.

HODGSON, J. (1982). Influence of sward characteristics on diet selection and herbage intake by the grazing animal. In *Nutritional limits to animal production from pastures*. Ed. Hacker,J.B. Farnham Royal: C.A.B.

HOLCOMBE, D.J., ROLAND, D.A. and HARMS, R.H. (1976). The ability of hens to regulate protein intake when offered a choice of diets containing different levels of protein. *Poult. Sci.* 55: 1731-1737.

HUXLEY, (1932). The Problems of Relative Growth. New York: Dial Press.

INRA (1978). Alimentation des ruminants. *Inst. Nat. de la Rec. Agron.* Versailles.

JACKSON, H.M., ROBINSON, D.W. AND KHALAF, F. (1970) Dietary animo acids and food selection by gilts. *J. Anim. Sci.* 31: 204.

JACKSON, T.H. (1967). The allometric relationship between carcase muscle and carcase bone in Scottish Blackface sheep. *Anim.Prod.* 9: 531-533.

JOHNSON, B.C., HAMILTON, T.S., MITCHELL, H.H. AND ROBINSON, W.B. (1942). The relative efficiency of urea as a protein substitute in the ration of ruminants. *J. Anim. Sci.* 1: 236-245.

JORDAN, W.H. (1906). The Feeding of Animals. New York.

KELLAWAY, R.C. (1973). The effects of nutrition, genotype and sex on growth , body composition and wool production in grazing sheep. *J. Agric. Sci. Camb.* 80: 17-27.

KELLNER, O. (1915). The scientific feeding of animals. London: Duckworth.

KEMPSTER, H.L. (1916). Food selection by laying hens. *J. Amer. Assoc. Invest. Poult. Husb.* 3: 26-28.

KEMPSTER, A.J. (1981). The EEC sheep meat regime - implications for lamb and hogget carcass production. MLC, Bletchley.

KEMPSTER, A.J. AND CUTHBERTSON, A. (1977). A survey of the carcass characteristics of the main types of British lamb. *Anim. Prod.* 25: 165-179.

KEENAN, D.M., McMANUS, W.R. AND FREER, M. (1969). Changes in body composition and efficiency of mature sheep during loss and regain of liveweight. *J. Agric. Sci. Camb.* 72: 139-171.

KENNEY, P.M. AND BLACK, J.L. (1984). Factors affecting diet selection by sheep. I. Potential intake rate and acceptability of feed. *Aust. J. Agric. Res.* 35: 551-563.

KIRKWOOD, J.K. AND PRESCOTT, N.J. (1984). Growth rate and pattern of gut development in mammals and birds. *Lives. Prod. Sci.* II: 461-474.

KLEIBER, M. (1961). The Fire of Life: an introduction to animal energetics. Univ. Calif., Davis: John Wiley & Sons.

KON, S.K. (1931). The self-selection of feed constituents by the rat. *Biochem J.* 25: 473-481.

KREBS, J.R. AND McCLEERY, H. (1984). Optimisation in behavioural ecology, in *Behavioural Ecology - an evolutionary approach.* Chap. 4, 2nd Ed. Blackwell, Oxford. edited by Krebs, J.R. and Davies, N.B.

KYRIAZAKIS, I., EMMANS, G. AND WHITTEMORE, C.T. (1987) Single and choice-feeding of pigs as methods of investigating their ability to control protein intake. *Anim.Prod.* 44: 462.

LATIF, M.G.A. AND OWEN, E. (1980). A note on the growth performance and carcass composition of Texel- and Suffolk-Sired lambs in an intensive feeding system. *Anim. Prod.* 30: 311-314.

LAIRD, A.K. (1966) Postnatal growth of birds and mammals *Growth* 30: 349-363.

LAIRD, A.K., TYLER, S.A., AND BARTON, A.D. (1965). Dynamics of Normal growth. *Growth* 29: 233-248.

LAWES, J.B. AND GILBERT, J.H. (1859). Experimental Inquiry into the composition of some of the animals fed and slaughtered as human food. *Phil. Trans. Roy. Soc. Pt. II* 493-678.

LAWES, J.B. AND GILBERT, J.H. (1860). On the composition of oxen, sheep and pigs, and of their increase whilst fattening. *J. Roy. Agric. Soc. Eng* 21: 433-488.

LAWLOR, M.J., CARROLL, M.A., AND POOLE, D.B.R. (1976). Effects of restricted

postnatal nutrition on the growth rate and carcass consumption of fattening lambs. *Proc. Brit. Soc. Nutr.* 35 (1): 12A.

LAWRENCE, T.L.J. AND PEARCE, J. (1964). Some effects of wintering beef cattle on different planes of nutrition. *J. Agric. Sci. Camb.* 63: 5-21.

LEUNG, P.M.B., ROGERS, Q.R. AND HARPER, A.E. (1968). Effect of amino acid imbalance on dietary choice in the rat. *J. Nutr.* 95: 483-92.

LITTLE, D.A. AND SANDLAND, R.L. (1975). Studies on the distribution of body fat in sheep during continuous growth, and following nutritional restriction and rehabilitation. *Austl. J. Agric. Res.* 26: 363-374.

LLOYD, M. (1983). An evaluation of commercial store lamb finishing systems. Paper to JCO committee.

LLOYD, M., EMMANS, G.C. AND PRESCOTT, J.H.D. (1985). The effect of nutrition and stage of maturity on the efficiency of lamb growth and carcass quality. *Anim. Prod.* 40: 522.

MADSEN, J. (1985). The basis for the proposed Nordic Protein Evaluation System for ruminants. The AAT-PBV System. *Acta Agriculturae Scandinavica Supplementum* 25: 9-20.

McCLELLAND, T.H. AND RUSSELL, A.J.F. (1972). The distribution of body fat in Scottish Blackface and Finnish Landrace lambs. *Anim. Prod.* 15: 301-306.

McCLELLAND, T.H., BONAITI, B. AND TAYLOR, St.C.S. (1976). Breed differences in body composition of equally mature sheep. *Anim. Prod.* 23: 281-293.

McMEEKAN, C.P. (1940). Growth and development in the pig, with special reference to carcass quality character. I. 276-344.

II. The influence of the plane of nutrition on growth and development. *J. Agric. Sci. Camb.* 30: 387-436.

III. The effect of plane of nutrition on the form and composition of the bacon pig. *J.Agric. Sci. Camb.* 30: 511-569.

IV. The use of sample joints and of carcass measurement as indices of the composition of the bacon pig. V. The bearing of the main principles emerging upon the many problems of animal production and human development. *J. Agric. Sci. Camb.* 31: 1-49.

McMANUS, W.R., REID, J.T. AND DONALDSON, L.E. (1972) Studies of compensatory growth in sheep. *J. Agric. Sci. Camb.* 79: 1-12.

MARSTON, H.R. (1935) Studies on the relationship between nutrition and wool production. *J. Agric. Sci. Camb.* 25: 103-131.

MITCHELL, H.H., KAMMLADE, W.G. AND HAMILTON, T.S. (1928). A technical study of the maintenance and fattening of lambs and their utilisation of a ration of alfalfa hay and corn. *Bull. Ill. Agric. Exp. Sta.* 314.

MITCHELL, H.S. AND MENDEL, L.B. (1921) The choice between adequate and

inadequate diet, as made by rats and mice. *Amer. J. Physiol* 58: 211-225.

MEYER, J.H. AND CLAWSON, W.J. (1964). Undernutrition and subsequent realimentation in rats and sheep. *J. Anim. Sci.* 23: 214-224.

MOORE, A.J. (1985). A mathematical equation for animal growth from embryo to adult. *Anim. Prod.* 40: 441-453.

MOORE, R.W. AND DOLLING, D.H.S. (1961). Ability to select diet in Merino sheep fed in pens. *Aust. J. Exp. Agric. Anim. Husb.* 1: 15-17.

MORGAN, J.A. AND OWEN, J.B. (1972). The nutrition of artificially reared lambs.

1. The effect of different feeding methods applied at three stages of growth. *Anim. Prod.* 15: 285-293.

2. The effect of feed restriction at three stages of growth on growth and carcass composition. *Anim.Prod.* 15: 293-300.

3. The effect of sex on the performance and carcass composition of lambs subjected to different nutritional treatments. *Anim.Prod.* 16: 49-57.

MORE O'FERRAL, G.J. AND TIMON, V.M. (1977). A comparison of eight sire breeds for lamb production. 1. Lamb growth and carcass measurements. *Ir. J. Agric. Res.* 16: 267-75. 2. Lamb carcass composition. 16: 277-84.

MOULTON, C.R., TROWBRIDGE, P.F. AND HAIGH, L.D. (1921). Studies in Animal Nutrition. I. Changes in Form and Weight on Different Planes of Nutrition. *Missouri. Agric. Exp. Sta. Res. Bull.* 43.

MOULTON, C.R., TROWBRIDGE, P.F. AND HAIGH, L.D. (1922). Studies in Animal Nutrition.

II. Changes in Proportions of Carcass and Offal on Different Planes of Nutrition. *Missouri Agric. Exp. Sta. Res. Bull.* 54.

III. Changes in Chemical Composition on Different Planes of Nutrition. *Missouri Agric. Exp. Sta. Res. Bull.* 55.

MURRAY, D.M. AND SLEZACECK, O. (1976) Growth rate and its effect on empty body weight, carcass weight and dissected carcass composition of sheep. *J. Agric. Sci. Camb.* 87: 171-179.

MUSTEN, B., PEACE, D. AND ANDERSON, G.H. (1974). Food intake regulation in the weanling rat: self-selection of protein and energy. *J. Nutr.* 104: 563- 572.

NOTTER, D.R., FERRELL, C.L., AND FIELD, R.A. (1984). Effects of breed and intake level on growth and feed efficiency in ram lambs. *J. Anim. Sci.* 58 (3) 560-576.

NRC (1985). Nutrient requirements of sheep. Sixth ed. *National Research Council*, National Academy Press, Washington, U.S.A.

OLDHAM, J.D. AND WEBSTER, A.J.F. (1986). Paper presented at the EAAP

Annual Meeting, Budapest.

OSBORNE, T.B. AND MENDEL, L.B. (1914). The suppression of growth and the capacity to grow. *J. Biol. Chem.* 18: 95-106.

OSBORNE, T.B. AND MENDEL, L.B. (1915). The resumption of growth after long continued failure to grow. *J. Biol. Chem.* 23: 439-454.

OSBORNE, T.B. AND MENDEL, L.B. (1916). Acceleration of growth after retardation. *Am. J. Physiol.* 40: 16-20.

OSBORNE, T.B., AND MENDEL, L.B. (1918). The choice between adequate and inadequate diets, as made by rats. *J. Biol. Chem.* 35: 19-27.

OSIKOWSKI, M. AND BORYS, B. (1976). Effect on production and carcass quality characteristics of wether lambs of crossing Blackheaded mutton, Ile de France and Texel rams with Polish Merino ewes. *Lives. Prod. Sci.* 3: 343-349.

OWEN, J.B. DAVIES, D.A.R. AND RIDGMAN, W.J. (1969). The control of voluntary food intake in ruminants. *Anim. Prod.* 11: 511-20.

PALSSON, H. (1940). Meat qualities in the sheep with special reference to Scottish breeds and crosses. III. Comparative development of selected individuals of different breeds and crosses as lambs and hoggets. *J. Agric. Sci. Camb.* 30: 1-82.

PALSSON, H. (1955). Conformation and body composition. In *Progress in the physiology of farm animals* Ed. Hammond, J. London:Butterworths.

PALSSON, H. AND VERGES, J.B. (1952). Effects of the plane of nutrition on growth and development of carcass quality in lambs.

I. The effects of high and low planes of nutrition at different ages. *J. Agric. Sci. Camb.* 42: 1- 92.

II. Effects on lambs of 30 lb. carcass weight. *J. Agric. Sci. Camb.* 42: 93-149.

PARKS, J.R. (1982). A Theory of Feeding and Growth of Animals. Berlin: Springer-Verlag.

PAMP, D.E., GOODRICH, R.D. AND MEISKE, J.C. (1977). Free choice minerals for lambs fed calcium- or sulphur-deficient rations. *J. Anim. Sci* 45: 1458-1466.

POMEROY, R.W. (1955). Liveweight growth. In *Progress in the physiology of farm animals* Ed. Hammond,J. London: Butterworths.

PRESCOTT, J.H.D. (1981). The future for poultry in animal production. Paper presented at the Scottish Poultry Conference.

RANHOTRA, G.S. AND JORDAN, R.M. (1966). Protein and energy requirements of lambs weaned at six to eight weeks of age as determined by growth and digestion studies. *J. Anim. Sci.* 25: 630-635.

RATTRAY, P.V., GARRETT, W.N., MEYER, H.H., BRADFORD, G.E., EAST, N.E. AND HINMAN, N. (1973). Body and carcass composition of Targhee and Finn-Targhee

lambs. *J. Anim. Sci.* 37 (4) : 892-897.

RHODES, D.N. (1969) Meat production from entire male animals. London:Churchill.

RICHTER, C.P., HOLT, L.E. AND BARELARE, B. (1938). Nutritional requirements for normal growth and reproduction in rate studied by the self-selection method. *Amer. J. Physiol* 122: 734-744.

ROBERTSON, T.B. (1923) The Chemical Basis of Growth and Senescence. Philadelphia: Lippincott.

ROBINSON, D.W.(1974). Food intake regulation in pigs. III. Voluntary food selection between protein-free and protein-rich diets. *Br. Vet. J.* 130: 522-527.

ROBINSON, D.W. (1975). Food intake regulation in pigs. V. The influence of dietary animo acid pattern of free choice food selection in pigs. *Br. Vet. J.* 131: 707-714.

ROBINSON, J.J. AND McDONALD, I. (1979). Ovine prenatal growth, its mathematical description and the effects of maternal nutrition. *Ann. Biol. Anim. Bioch. Biophys.* 19 (1B) 225-234.

ROSE, S.P. AND MICHIE, W. (1982). The food intakes and growth of choice-fed turkeys offered balanced mixtures of different compositions. *Br. Poult. Sci.* 23: 547-554.

RUGG, W.C. (1925). Feeding experiments, free choice of feeds. *Vict. Aust. Dept. Agric. Bull.* 54: 36-56.

RUSSEL, A.J.F., DONEY, J.M. AND GUNN, R.G. (1971). The distribution of chemical fat in the bodies of Scottish Blackface ewes. *Anim.Prod.* 13: 503-509.

RYDER, M.L. AND STEPHENSON, S.K. (1968). Wool growth. London: Academic Press.

SCHMIDT-NIELSEN, K. (1984) Scaling. Why is animal size so important? Camb. U. Press.

SCOTT, E.M. (1946). Self-selection of diet. I. Selection of purified components. *J. Nutr.* 31: 397.

SCOTT, E.M. AND QUINT, E. (1946). Self-selection of diet. IV. Appetite for protein. *J. Nutr.* 32: 293-302.

SEARLE, T.W., GRAHAM, N. M. AND CALLAGHAN, M. (1972). Growth in sheep. I. The chemical composition of the body. *J. Agric. Sci. Camb.* 79: 371-382.

SEARLE, T.W. AND GRAHAM, N. M. (1975). Studies of weaned sheep during and after a period of weight stasis. II. Body composition. *Aust. J. Agric.* 26: 355-361.

SEARLE, T.W. GRAHAM, N.M. AND SMITH, E. (1979). Studies of weaned lambs before, during and after a period of weight loss. II. Body composition. *Aust. J. Agric. Res.* 30: 525-531.

SEARLE, T.W. AND GRIFFITHS, D.A. (1976). The body composition of growing sheep during milk feeding and the effect on composition of weaning at various body weights. *J.Agric. Sci. Camb.* 86:483-486.

SEARLE, T.W. AND GRIFFITHS, D.A. (1983). Equations for postnatal chemical composition of the fat-free emtpy body of sheep and cattle. *J. Agric. Sci. Camb.* 100: 693-699.

SPEEDY, A.W. (1977). Lamb finishing on forage crops. Paper presented to "Farming under pressure" conference, Ingliston, Edinburgh.

STABLER, A.L. (1911). Hopper feeding: A preliminary test. *Maryland Agr. Exp. Stat. Bul.* 150: 108-113.

TAYLOR, St.C.S. (1965). A relationship between mature weight and time taken to mature in mammals. *Anim. Prod.* 7: 203-220.

TAYLOR, St.C.S. (1968). Time taken to mature in relation to mature weight for sexes, strains and species of domesticated mammals and birds. *Anim. Prod.* 10: 157-169.

TAYLOR, St.C.S. (1980a). Genetic size-scaling rules in animal growth. *Anim. Prod.* 30: 161-165.

TAYLOR, St.C.S (1980b). Genetically standardised growth equations. *Anim. Prod.* 30: 167-175.

TAYLOR, St.C.S. (1980c). Live-weight growth from embryo to adult in domesticated mammals. *Anim. Prod.* 31: 223-235.

THERIEZ, M., TISSIER, M. AND ROBELIN, J. (1981). The chemical composition of intensively fed lambs. *Anim. Prod.* 32: 29-37.

THOMPSON, D.W. (1917). On Growth and Form. Cambridge.

THORNTON, R.F., HOOD, R.L., JONES, P.N. AND RE, V.M. (1979). Compensatory growth in sheep. *Aust. J. Agric. Res.* 30: 135-151.

TULLIS, J.B. (1982). Protein growth in pigs. PhD Thesis, University of Edinburgh.

VAN SOEST, P.J. (1965). Symposium on factors influencing the voluntary intake of herbage by ruminants (Voluntary intake in relation to chemical composition and digestibility.) *J. Anim. Sci.* 24: 834-843.

VESELY, J.A. AND PETERS, H.F. (1972). Muscle, bone and fat and their interrelations in five breeds of lamb. *Can. J. Anim. Sci.* 52: 629-636.

VOHRA, P. AND HEIL, J.R. (1969). Selection of zinc-supplemented diets by turkey poults. *Poult. Sci.* 48: 1118-1120.

WALDO, D.R. (1986). Symposium: Forage utilisation by the lactating cow. (Effect of forage quality on intake and forage-concentrate interactions) *J. Dairy Sci.* 69: 617-631.

WALLACE, H.D., PALMER, A.Z. CARPENTER, J.W. AND COMBS, G.E. (1973). By choice gilts consume more protein than barrows. *J. Anim. Sci.* 36: 203.

WALLACE, L.R. (1948). The growth of lambs before and after birth in relation to feeding level. *J. Agric. Sci. Camb.* 38: 1-93.

WARDROP, I.D. AND COOMBE, J.B. (1960). The post-natal growth of the visceral organs of the lamb. I. The growth of the visceral organs of the grazing lamb from first to sixteen weeks of age. *J. Agric. Sci.* 54: 140-143.

WARDROP, I.D. (1960). The post-natal growth of the visceral organs of the lamb. II. The effect of diet on growth rate, with particular reference to the parts of the alimentary tract. *J. Agric. Sci.* 55: 127-131.

WATERS, H.J. (1908). The capacity of animals to grow under adverse conditions. *30th Proc. Soc. Prom. Agric. Sci. N.Y.*

WHITTEMORE,C.T. AND TULLIS,J.B. (1987). Protein growth in pigs. *Anim.Prod.* 44: 462.

WILCKENS, (1865) *J. Landw.* 10, cited by Hammond (1932), p.95.

WILSON, P.N. (1952,1954a,b). Growth Analysis of the domesticated fowl. I.The effect of plane of nutrition and sex on live-weights and external measurements. *J. Agric. Sci. Camb.* 42: 369-381.

II. The effect of plane of nutrition on carcass composition. *J. Agric. Sci. Camb.* 44: 67-85.

III. The effect of plane of nutrition on carcass composition of cockerels and egg yields of pullets. *J. Agric. Sci. Camb.* 45: 110-124.

WILSON, P.N. (1958). The effect of plane of nutrition on the growth and development of the East African Dwarf Goat. I. The effect of plane of nutrition on the live-weight gains and external measurements of kids. *J. Agric. Sci. Camb.* 50: 198-210.

II. Age changes in carcass composition of female kids. *J. Agric. Sci. Camb.* 51: 4-21.

WILSON, P.N. AND OSBOURN, D.F. (1960). Compensatory growth after undernutrition in mammals and birds. *Biol. Revs.* 35: 324-363.

WINCHESTER, C.F. AND ELLIS, N.R. (1957). Delayed growth in beef cattle. *Tech. Bull. U.S. Dep. Agric.* 1159.

WINTER, W.H., TULLOH, N.M. AND MURRAY, D.M. (1976). The effect of compensatory growth in sheep on empty body weight, carcass weight and the weights of some offals. *J. Agric. Sci. Camb.* 87: 433-441.

WOLF, B.T., SMITH, C. AND SALES, D.I. (1980). Growth and carcass composition in the crossbred progeny of six terminal sire breeds of sheep. *Anim. Prod.* 31: 307-313.

WOOD, J.D., MACFIE, H.J.H. POMEROY, R.W. AND TWINN, D.J. (1980). Carcass

composition in four sheep breeds: the importance of type of breed and stage of maturity. *Anim. Prod.* 30: 135-152.

WOOD-GUSH, D.G.M. AND KARE, M.R. (1966). The behaviour of calcium-deficient chickens. *Br. Poult. Sci.* 7: 285-290.

WRIGHT, S. (1926). Book review. *J. Amer. Stat. Soc.* 21: 493-497. in Laird *et al*, 1965.

APPENDIX B
LIVEWEIGHT AND FEED INTAKE DATA -- EXP.1

Lamb identities (L) are given in Table 2.6.

LIVEWEIGHT (kg)

				WEEKS						
L	W0	W1	W2	W3	W4	W5	W6	W7	W8	W9	W10
1	25.4	27.4	28.9	32.0	34.5	37.1	39.1	41.9	43.5	44.3	46.1
9	24.4	24.9	27.4	30.8	32.3	33.6	35.2	40.2	39.6	43.3	42.1
2	25.5	29.0	31.0	33.4	36.2	38.2	41.8	44.7	45.9	45.8	47.4
8	22.7	24.6	28.5	30.5	31.4	31.4	34.9	36.2	40.3	40.8	43.0
3	25.5	28.0	30.5	32.2	35.1	37.6	37.4	41.1	43.0	43.6	44.7
12	27.1	30.1	31.5	34.2	38.6	41.3	42.1	40.9	43.0	44.5	47.8
4	25.9	27.3	28.7	31.0	34.2	36.2	38.8	43.6	44.4	48.2	51.6
10	26.8	27.8	30.1	32.2	35.0	36.0	38.0	41.0	40.7	44.0	46.2
5	25.3	24.4	26.3	30.6	32.6	35.5	37.0	38.5	40.3	39.8	43.7
7	20.7	22.8	26.0	26.9	31.6	34.4	36.3	38.2	39.7	43.1	45.0
6	25.5	27.0	27.1	29.9	32.4	35.0	34.3	36.0	37.6	37.8	39.7
11	24.1	25.4	26.8	29.2	32.8	34.5	34.0	37.9	39.5	42.4	43.4

FEED INTAKES

F(A) = weekly intake of feed A (kg).
F(X) = weekly intake of feed B, C or D (kg).
F(T) = total weekly feed intake (kg).

PERIOD I

L		W1	W2	W3	W4
1	F(A)	0.54	1.73	1.38	1.74
	F(X)	6.25	6.09	7.89	8.62
	F(T)	6.79	7.82	9.27	10.36
9	F(A)	1.15	0.31	0.01	0.04
	F(X)	2.78	5.77	8.11	10.14
	F(T)	3.93	6.08	8.12	10.18
2	F(A)	0.21	0.66	1.07	0.16
	F(X)	7.83	7.50	9.03	11.81
	F(T)	8.04	8.16	10.10	11.97
8	F(A)	1.06	1.04	0.88	1.92
	F(X)	6.31	7.55	8.08	6.85
	F(T)	7.37	8.59	8.96	8.77
3	F(A)	2.18	2.17	0.92	2.00
	F(X)	6.56	8.41	10.25	9.51
	F(T)	8.74	10.58	11.17	11.51
12	F(A)	1.69	2.60	1.83	1.93
	F(X)	7.04	7.49	8.31	10.64
	F(T)	8.73	10.09	10.14	12.57
4	F(A)	0.99	2.38	3.69	7.94
	F(X)	6.87	5.61	3.81	0.50
	F(T)	7.86	7.99	7.50	8.44
10	F(A)	0.58	0.13	0.86	0.18
	F(X)	8.50	9.42	9.01	11.43
	F(T)	9.08	9.55	9.87	11.61
5	F(A)	2.09	5.02	5.63	5.25
	F(X)	1.41	0.03	1.74	5.75
	F(T)	3.50	5.05	7.37	11.00

L		W1	W2	W3	W4
7	F(A)	0.26	1.04	1.22	3.28
	F(X)	3.54	7.38	8.85	8.54
	F(T)	3.80	8.42	10.07	11.82
6	F(A)	7.07	6.12	1.41	0.56
	F(X)	0.73	1.73	7.60	8.81
	F(T)	7.80	7.85	9.01	9.37
11	F(A)	3.60	0.37	0.57	0.05
	F(X)	1.53	7.97	7.15	10.15
	F(T)	5.13	8.34	7.72	10.20

		PERIOD II				PERIOD III	
L		W5	W6	W7	W8	W9	W10
1	F(A)	7.48	11.65	8.94	8.71	6.47	8.03
	F(X)	3.74	1.53	2.96	4.94	6.67	5.46
	F(T)	11.22	13.18	11.90	13.65	13.14	13.49
9	F(A)	0.26	0.06	0.22	3.15	10.44	5.79
	F(X)	11.10	12.58	9.75	10.28	2.83	4.32
	F(T0	11.36	12.64	9.97	13.43	13.27	10.11
2	F(A)	0.22	1.61	5.38	4.50	4.12	3.42
	F(X)	10.67	11.16	5.78	6.71	6.91	8.59
	F(T)	10.89	12.77	11.16	11.21	11.03	12.01
8	F(A)	1.63	3.34	5.71	9.14	8.54	9.00
	F(X)	4.83	6.67	3.40	1.79	3.43	2.14
	F(T)	6.46	10.01	9.11	10.93	11.97	11.14
3	F(A)	1.15	0.69	0.59	0.55	2.08	1.69
	F(X)	11.44	11.05	10.88	11.11	8.91	8.63
	F(T)	12.59	11.74	11.47	11.66	10.99	10.32
12	F(A)	5.59	5.01	2.03	1.27	0.08	3.20
	F(X)	7.83	6.77	6.36	9.46	11.32	7.94
	F(T)	13.42	11.78	8.39	10.73	11.40	11.14
4	F(A)	0.43	0.78	1.20	0.33	5.25	6.09
	F(X)	10.05	11.39	10.14	13.30	9.20	9.28
	F(T)	10.48	12.17	11.34	13.63	14.45	15.37
10	F(A)	0.01	0.74	9.61	5.04	10.21	11.47
	F(X)	10.27	9.92	2.48	5.72	1.62	0.42
	F(T)	10.28	10.66	12.09	10.76	11.83	11.89
5	F(A)	4.98	4.15	2.98	3.35	2.95	0.46
	F(X)	7.04	7.25	7.01	6.54	5.85	10.43
	F(T)	12.02	11.40	9.99	9.89	8.80	10.89
7	F(A)	1.71	1.06	0.72	1.78	6.65	8.53
	F(X)	11.75	11.14	11.02	9.54	4.72	4.73
	F(T)	13.46	12.20	11.74	11.32	11.37	13.26
6	F(A)	0.54	0.44	1.73	3.06	4.33	2.82
	F(X)	8.82	8.39	6.48	5.14	4.23	6.02
	F(T)	9.36	8.83	8.21	8.20	8.56	8.84
11	F(A)	0.85	0.95	0.75	0.60	1.57	4.27
	F(X)	10.37	9.19	9.29	8.63	9.39	5.60
	F(T)	11.22	10.14	10.04	9.23	10.96	9.87

APPENDIX C
LIVEWEIGHT AND FEED INTAKE DATA -- EXP. 2

Treatments (T) are those given in Table 2.10.

LIVEWEIGHT (kg) WEEK

L	W0	W1	W2	W3	W4	W5	W6	W7	W8	W9	W10
T1											
1	23.4	28.8	31.6	33.8	36.8	39.2	41.3	44.1	46.9	52.0	51.6
2	18.5	17.3	19.5	22.8	24.7	27.9	30.8	32.8	35.8	37.4	39.5
3	22.0	22.3	25.9	26.9	31.3	33.3	37.2	38.9	40.0	42.3	44.0
4	20.3	23.6	26.0	29.2	32.7	34.1	35.5	38.9	39.7	39.2	40.0
T2											
5	20.0	23.5	25.4	28.1	29.2	33.6	35.5	36.3	39.4	42.8	42.5
6	17.9	19.6	22.9	25.6	23.5	27.3	29.5	31.8	33.2	36.2	37.9
7	19.9	21.6	24.6	28.6	31.0	34.6	36.1	40.0	43.1	44.2	49.4
8	20.1	19.7	21.7	25.4	27.7	29.4	31.4	31.5	34.2	37.0	38.6
T3											
9	21.4	24.6	28.2	29.9	33.1	34.4	38.9	40.5	43.5	44.3	48.0
10	23.3	23.2	25.7	25.2	27.7	30.4	32.7	33.4	33.5	37.5	38.3
11	15.9	14.6	16.5	19.1	22.0	25.1	28.0	30.1	31.8	35.0	36.1
12	19.8	19.8	22.9	27.0	29.0	30.9	34.6	37.6	39.7	40.6	44.6
T4											
13	19.7	20.6	25.3	28.3	30.9						
14	20.6	23.0	24.7	27.8	30.0						
15	18.1	19.0	19.5	22.7	24.7						
16	20.6	22.6	27.4	29.7	32.3						
T5											
46	19.6	21.2	23.8	26.7	30.3	32.3	35.9	36.8	38.8	41.4	43.5
47	17.1	18.0	20.4	22.5	24.9	25.5	28.1	30.7	33.5	34.4	36.1
48	18.5	21.6	24.8	27.4	31.6	33.1	37.7	38.7	41.6	41.7	42.2
T6											
41	17.6	19.5	21.7	23.6	26.0	29.1	32.6	34.1	36.8	38.7	41.4
42	21.1	24.0	25.5	28.0	30.9	32.8	33.4	35.5	38.3	40.2	41.1
43	16.3	15.1	16.9	19.2	20.7	21.9	24.4	26.7	30.7	32.7	34.0
44	20.3	19.7	22.2	24.7	25.9	27.9	31.1	33.5	36.5	38.8	39.1

L	W11	W12	W13	W14	W15	W16	W17	W18	W19	W20	W21
T1											
1	51.5	55.3	57.2	59.0	59.2	59.3	59.0	60.7	63.4	66.2	69.1
2	40.6	42.3	44.2	47.7	49.3	50.4	52.1	51.6	54.8	57.3	59.0
3	44.8	48.0	48.8	47.6	49.4	52.4	51.7	53.7	56.4	58.3	63.1

FEED INTAKES

F(A) is the weekly intake of feed A (kg).
F(B), F(C) and F(D) is the weekly intake of feeds B, C and D respectively.
F(T) is the total weekly feed intake (kg).

L		W1	W2	W3	W4	W5	W6	W7
T1								
1	F(A)	4.80	5.68	1.99	5.94	7.82	8.00	9.75
	F(B)	1.68	4.14	8.76	9.10	7.00	5.16	6.80
	F(T)	6.48	9.82	10.75	15.04	14.82	13.16	16.55
2	F(A)	1.48	3.90	4.79	5.64	6.63	6.45	6.23
	F(B)	1.90	0.69	3.89	3.93	4.08	3.78	5.44
	F(T)	3.38	4.59	8.68	9.57	10.71	10.23	11.67
3	F(A)	1.71	2.79	4.16	4.36	2.76	2.87	2.74
	F(B)	3.03	4.12	3.66	5.79	8.11	8.22	8.44
	F(T)	4.74	6.91	7.82	10.15	10.87	11.09	11.18
4	F(A)	1.03	0.86	2.37	1.76	1.81	1.41	1.85
	F(B)	3.74	7.49	8.62	10.24	10.00	10.49	8.51
	F(T)	4.77	8.35	10.99	12.00	11.81	11.90	10.36
T2								
5	F(A)	1.89	3.66	3.56	3.87	4.41	4.47	5.87
	F(C)	1.49	4.09	5.78	5.37	5.83	7.00	5.94
	F(T)	3.38	7.75	9.34	9.24	10.24	11.47	11.81
6	F(A)	3.43	6.86	7.20	2.29	5.69	5.31	6.68
	F(C)	2.13	3.69	2.97	1.54	3.48	4.98	4.07
	F(T)	5.56	10.55	10.17	3.83	9.17	10.29	10.75
7	F(A)	4.43	7.81	9.85	10.23	11.84	10.39	11.47
	F(C)	0.51	0.45	0.39	0.77	2.53	2.91	3.20
	F(T)	4.94	8.26	10.24	11.00	14.37	13.30	14.67
8	F(A)	3.31	4.41	5.60	4.17	6.21	7.44	7.56
	F(C)	0.53	1.18	2.50	4.30	2.80	2.24	1.54
	F(T)	3.84	5.59	8.10	8.47	9.01	9.68	9.10
T3								
9	F(A)	4.48	7.62	8.10	8.40	9.58	12.00	13.42
	F(D)	0.66	1.02	1.19	1.72	2.03	1.74	1.30
	F(T)	5.14	8.64	9.29	10.12	11.61	13.74	14.72
10	F(A)	4.74	4.92	3.56	4.61	5.59	7.06	7.31
	F(D)	0.39	1.43	0.78	1.70	3.27	2.73	2.19
	F(T)	5.13	5.06	4.34	6.31	8.86	9.79	9.50
11	F(A)	2.11	5.29	5.80	6.36	7.50	8.47	8.36
	F(D)	0.00	0.20	0.52	1.63	1.85	2.21	2.47
	F(T)	2.11	5.49	6.32	7.99	9.35	10.28	10.83
12	F(A)	0.79	3.78	7.56	7.82	7.65	10.16	12.50
	F(D)	0.01	0.76	0.63	0.91	0.81	0.60	0.60
	F(T)	0.80	4.54	8.19	8.73	8.46	10.76	13.10

L		W1	W2	W3	W4	W5	W6	W7
T4								
13	F(B)	5.88	7.98	8.99	10.24			
	F(D)	0.67	0.13	0.50	0.22			
	F(T)	6.55	8.11	9.49	10.46			
14	F(B)	6.24	7.98	9.49	11.34			
	F(D)	0.16	0.00	0.23	0.28			
	F(T)	6.40	7.98	9.72	11.62			
15	F(B)	4.69	4.74	6.22	7.30			
	F(D)	0.23	0.73	0.58	0.76			
	F(T)	4.92	5.47	6.80	8.06			
16	F(B)	3.56	8.38	10.21	11.77			
	F(D)	0.07	0.01	0.00	0.11			
	F(T)	3.63	8.39	10.21	11.88			
T5								
46	F(B)	5.83	8.04	9.86	10.68	10.89	11.39	12.71
47	F(B)	3.39	5.52	6.32	7.50	8.50	9.97	9.74
48	F(B)	5.24	8.68	10.89	12.34	13.14	14.89	13.20
T6								
41	F(A)	4.00	7.20	8.41	9.47	10.64	11.93	10.27
42	F(A)	5.77	7.20	7.13	9.92	10.72	11.08	8.27
43	F(A)	1.86	3.51	5.64	6.45	8.01	9.77	8.91
44	F(A)	1.35	6.07	6.42	7.97	8.36	10.33	10.40

FEED INTAKES (WEEKS 8-14)

L		W8	W9	W10	W11	W12	W13	W14
T1								
1	F(A)	9.75	8.91	9.18	7.50	8.50	9.64	12.00
	F(B)	7.62	7.93	6.29	6.00	6.30	4.12	0.25
	F(T)	17.37	16.84	15.47	13.50	14.80	13.76	12.25
2	F(A)	5.95	4.94	5.71	5.26	5.93	7.54	9.56
	F(B)	6.32	5.54	5.33	6.19	4.89	4.62	2.48
	F(T)	12.27	10.48	11.04	11.45	10.82	12.16	12.04
3	F(A)	2.60	1.97	4.46	4.33	6.00	8.56	8.72
	F(B)	10.30	9.89	8.83	7.84	7.29	4.20	0.71
	F(T)	12.90	11.86	13.29	12.17	13.29	12.76	9.43
T2								
5	F(A)	6.70	7.72	8.78				
	F(C)	5.40	8.78	4.23				
	F(T)	12.10	16.50	13.01				
6	F(A)	7.88	8.52	9.00				
	F(C)	3.78	4.47	3.64				
	F(T)	11.6	12.99	12.64				
7	F(A)	11.44	12.53	11.64				
	F(C)	3.35	3.20	3.05				
	F(T)	14.79	15.73	14:69				
8	F(A)	10.23	10.71	10.70				
	F(C)	1.65	2.20	2.17				
	F(T)	11.88	12.91	12.87				

L		W8	W9	W10
T3				
9	F(A)	13.42	13.30	11.99
	F(D)	1.30	1.40	1.90
	F(T)	14.72	14.70	13.89
10	F(A)	7.31	6.28	6.89
	F(D)	2.19	1.64	3.00
	F(T)	9.50	7.92	9.89
11	F(A)	8.36	8.70	8.70
	F(D)	2.47	1.76	1.26
	F(T)	10.83	10.46	9.96
12	F(A)	12.50	13.40	12.00
	F(D)	0.61	0.63	1.20
	F(T)	13.11	14.03	13.20
T5				
46	F(B)	11.27	8.45	12.45
47	F(B)	9.74	8.93	11.30
48	F(B)	12.54	9.41	13.55
T6				
41	F(A)	13.27	13.98	13.48
42	F(A)	9.91	12.17	10.50
43	F(A)	11.66	12.46	11.30
44	F(A)	12.25	12.82	11.45

FEED INTAKES (WEEKS 15-21)

L		W15	W16	W17	W18	W19	W20	W21
T1								
1	F(A)	10.53	9.00	9.11	7.82	8.82	10.90	7.67
	F(B)	2.05	0.25	0.24	1.41	4.62	1.27	5.57
	F(T)	12.58	9.25	9.35	9.23	13.44	12.17	13.24
2	F(A)	9.33	8.00	8.62	8.00	7.34	7.93	7.24
	F(B)	2.97	1.20	2.98	3.01	5.22	2.58	3.58
	F(T)	12.30	9.20	11.60	11.01	12.56	10.51	10.82
3	F(A)	9.50	9.59	9.68	9.35	10.66	11.00	9.24
	F(B)	2.69	0.22	2.58	2.23	6.59	0.70	2.85
	F(T)	12.19	9.81	12.26	11.58	17.25	11.70	12.09

APPENDIX D
LIVEWEIGHT AND FEED INTAKE DATA -- EXP.3

Treatments are those given in Table 2.17.

LIVEWEIGHT (kg) WEEKS

L		W0	W1	W2	W3	W4	W5	W6
T1								
25	M	22.1	25.1	30.2	33.2	37.1	40.4	43.0
26	M	19.1	22.0	23.8	28.5	31.4	34.7	38.0
27	F	16.4	20.4	18.5	19.0	22.6	26.3	29.0
28	F	21.2	21.2	25.2	28.1	30.6	34.6	37.2
T2								
21	M	21.6	23.9	27.2	29.9	32.1	37.3	40.1
22	M	21.3	23.4	25.5	26.7	27.2	32.4	35.1
23	F	17.2	18.6	21.0	24.3	27.4	29.8	31.9
24	F	19.6	20.4	22.8	25.1	28.6	31.5	34.5
T3								
17	M	21.6	23.8	26.6	30.2	32.5	35.0	37.6
18	M	14.0	14.7	18.2		30.9	35.4	38.2
20	F	21.0	24.1	27.4	29.4	32.0	34.3	36.7
T4								
46	M	19.6	21.2	23.8	26.7	30.3	32.3	35.9
47	M	17.1	18.0	20.4	22.5	24.9	25.5	28.1
48	F	18.5	21.6	24.8	27.4	31.6	33.1	37.7
T5								
29	M	18.7	17.6	21.4	25.5	26.7	29.7	32.3
30	M	19.8	23.7	27.4	31.1	34.0	37.4	41.9
31	F	21.5	24.2	28.3	31.4	35.5	38.8	42.5
32	F	19.2	18.1	22.0	24.6	28.0	31.1	33.9
T6								
33	M	19.6	21.3	25.0	26.9	29.0	30.3	32.0
34	M	16.2	18.5	19.4	22.9	24.3	26.8	30.4
35	F	15.5	17.1	19.7	21.8	24.3	26.5	29.6
36	F	18.8	20.2	23.1	25.3	28.3	30.9	34.5
T7								
37	M	23.6	19.4	19.5	23.9	25.2	27.0	30.8
38	M	17.2	16.3	20.0	21.9	24.1	25.0	27.6
39	F	22.0	24.2	25.0	29.0	29.3	32.2	34.4
T8								
14	M					30.0	33.4	36.5
15	F					24.7	28.7	30.6
16	F					32.3	36.0	39.8

	WEEKS				
L	W7	W8	W9	W10	W11
T1					
25	41.8	44.2	45.8	47.9	47.2
26	38.5	44.8	46.3	49.1	52.3
27	30.8	33.1	34.7	38.1	40.5
28	39.1	41.4	42.8	44.5	46.7
T2					
21	41.1	44.6	44.7	45.9	44.0
22	35.1	41.0	42.7	45.4	47.3
23	33.7	36.9	38.9	41.3	42.9
24	36.9	38.6	41.8	44.3	46.2
T3					
17	39.5	42.1	43.5	46.0	46.2
13	39.6	40.0	43.5	45.7	47.4
20	38.3	36.8	39.5	39.4	41.1
T4					
46	36.8	38.8	41.4	43.5	43.0
47	30.7	33.5	34.4	36.1	38.0
48	38.7	41.6	41.7	42.2	43.7
T5					
29	33.3	35.7	37.7	40.0	40.3
30	42.8	43.1	46.2	47.1	48.2
31	44.7	47.0	47.9	51.9	52.3
32	36.1	37.7	39.8	41.6	42.5
T6					
33	33.2	35.0	33.6	33.4	34.4
34	31.5	34.1	35.5	38.0	40.6
35	29.8	33.3	34.5	36.6	36.8
36	35.2	40.3	38.0	43.0	44.2
T7					
37	32.0	33.6	37.9	39.8	42.2
38	29.7	32.0	33.3	36.7	38.4
39	36.0	38.6	40.4	40.1	40.7
T8					
14	35.8	41.2	43.4	45.8	47.7
15	32.9	34.6	34.9	37.3	38.4
16	41.4	43.1	45.9	48.4	49.8

FEED INTAKES

F(B) = weekly intake of feed B'(kg)
F(Z) = weekly intake of feed Z (kg).
F(Y) = weekly intake of feed Y (kg).
F(X) = weekly intake of feed X (kg)
F(T) = total weekly feed intake (kg)

L		W1	W2	W3	W4	W5	W6
T1							
25	F(B)	3.76	5.90	7.17	8.76	8.96	9.70
	F(Z)	2.02	5.97	6.99	6.65	7.53	7.01
	F(T)	5.78	11.87	14.16	15.41	16.49	16.71
26	F(B)	6.16	6.62	7.12	9.13	8.83	8.40
	F(Z)	0.29	1.23	3.34	3.51	3.06	5.61
	F(T)	6.45	7.85	10.46	12.64	11.89	14.01
27	F(B)	4.56	3.35	1.04	5.49	7.91	9.76
	F(Z)	1.67	1.56	0.62	1.86	2.54	1.81
	F(T)	6.23	4.91	1.66	7.35	10.45	11.57
28	F(B)	1.59	4.39	6.75	9.26	9.51	8.45
	F(Z)	1.36	3.58	4.01	3.68	4.31	4.17
	F(T)	2.95	7.97	10.76	12.94	13.82	12.62
T2							
21	F(B)	4.22	8.38	10.56	10.41	11.65	11.96
	F(Y)	0.28	0.77	1.02	2.02	3.67	3.73
	F(T)	4.50	9.15	11.58	12.43	15.32	15.69
22	F(B)	2.43	5.28	3.74	2.39	3.13	4.52
	F(Y)	2.39	3.83	2.76	4.68	7.84	9.36
	F(T)	4.82	9.11	6.50	7.07	10.97	13.88
23	F(B)	3.18	5.21	7.01	7.82	6.30	6.00
	F(Y)	0.53	1.52	1.86	2.47	4.62	5.30
	F(T)	3.71	6.73	8.87	10.29	10.92	11.30
24	F(B)	5.41	5.42	7.82	8.56	10.25	10.68
	F(Y)	0.13	1.36	1.92	0.83	1.69	3.24
	F(T)	5.54	6.78	9.74	9.39	11.94	13.92
T3							
17	F(B)	1.91	4.85	6.23	5.47	5.55	6.71
	F(X)	3.85	4.76	4.73	6.57	7.74	6.36
	F(T)	5.76	9.61	10.96	12.04	13.29	13.07
18	F(B)	1.43	4.16	4.72		0.82	7.94
	F(X)	0.48	1.27	3.13		3.44	7.63
	F(T)	1.91	5.43	7.85		4.26	15.57
20	F(B)	4.36	5.97	2.18	3.75	3.48	7.87
	F(X)	1.51	3.70	9.84	7.58	7.96	3.25
	F(T)	5.87	9.67	12.02	11.33	11.44	11.12
T4							
46	F(B)	5.83	8.04	9.86	10.86	10.89	11.39
47	F(B)	3.39	5.50	6.32	6.61	7.50	8.50
48	F(B)	5.24	8.68	10.89	12.34	13.14	14.89

L		W1	W2	W3	W4	W5	W6
T5							
29	F(X)	3.19	7.09	10.79	11.00	11.27	11.65
30	F(X)	6.67	10.13	13.00	13.58	14.75	15.52
31	F(X)	7.04	10.60	12.15	13.21	14.05	15.07
32	F(X)	2.72	7.57	10.01	11.59	12.10	12.39
T6							
33	F(Y)	3.54	7.77	9.63	10.69	9.66	9.50
34	F(Y)	5.57	6.46	8.83	9.74	10.97	12.86
35	F(Y)	4.03	6.63	8.61	10.10	11.39	12.20
36	F(Y)	6.05	7.94	9.92	11.22	10.99	14.03
T7							
37	F(Z)	0.11	0.43	3.74	8.61	11.44	12.49
38	F(Z)	2.34	6.03	7.81	9.09	9.29	9.82
39	F(Z)	5.06	7.80	9.89	11.02	12.66	14.08
T8							
14	F(X)					13.90	14.54
	F(Z)					1.07	0.00
	F(T)					14.97	14.54
15	F(X)					10.30	11.81
	F(Z)					0.28	0.08
	F(T)					10.58	11.89
16	F(X)					12.44	15.19
	F(Z)					1.94	1.25
	F(T)					14.38	16.44

FEED INTAKES (WEEKS 7-11)

L		W7	W8	W9	W10	W11
T1						
25	F(B)	6.46	8.31	6.74	6.44	3.51
	F(Z)	4.98	6.01	5.98	5.48	5.98
	F(T)	11.44	14.32	12.72	11.92	9.49
26	F(B)	9.25	10.10	8.82	8.56	9.82
	F(Z)	6.03	5.57	6.86	6.28	5.94
	F(T)	15.28	15.67	15.68	14.84	15.76
27	F(B)	8.87	7.76	8.38	8.31	8.62
	F(Z)	2.55	2.88	3.41	4.29	4.42
	F(T)	11.42	10.64	11.79	12.60	13.04
28	F(B)	10.08	9.41	8.99	7.40	7.73
	F(Z)	3.40	4.07	3.86	4.44	3.98
	F(T)	13.48	13.48	12.85	11.84	11.71

L		W7	W8	W9	W10	W11
T2	F(B)	10.59	9.43	9.14	8.19	8.87
21	F(Y)	4.09	4.17	2.73	2.05	1.48
	F(T)	14.68	13.60	11.87	10.24	10.35
22	F(B)	7.14	8.19	9.08	8.89	8.64
	F(Y)	7.52	6.01	5.09	4.95	5.01
	F(T)	14.66	14.20	14.17	13.84	13.65
23	F(B)	8.56	8.32	8.19	8.45	8.97
	F(Y)	3.55	4.66	3.46	6.32	4.05
	F(T)	12.11	12.98	11.65	14.77	13.02
24	F(B)	10.72	9.87	7.86	7.99	9.16
	F(Y)	2.88	4.42	5.42	3.99	5.68
	F(T)	13.60	14.29	13.28	11.98	14.84
T3						
17	F(B)	7.41	7.16	6.71	6.50	6.42
	F(X)	5.17	5.33	5.11	7.77	6.26
	F(T)	12.58	12.49	11.82	14.27	12.68
13	F(B)	8.21	6.29	8.80	6.84	6.94
	F(X)	7.21	7.81	5.70	8.23	9.67
	F(T)	15.42	14.10	14.50	15.07	16.61
20	F(B)	8.00	6.79	8.31	6.69	3.11
	F(X)	2.91	2.52	3.09	2.29	6.51
	F(T)	10.91	9.31	11.40	8.98	9.62
T4						
46	F(B)	12.71	11.27	8.45	12.45	10.82
47	F(B)	9.97	9.74	8.93	11.30	10.82
48	F(B)	13.20	12.54	9.41	13.55	13.20
T5						
29	F(X)	10.47	11.16	11.72	10.54	10.17
30	F(X)	13.57	14.74	14.54	12.62	13.57
31	F(X)	14.69	14.88	14.88	14.86	14.67
32	F(X)	12.73	13.13	12.53	13.08	10.93
T6						
33	F(Y)	9.18	7.53	5.65	3.67	4.78
34	F(Y)	14.49	14.77	11.91	14.74	15.32
35	F(Y)	11.14	12.31	11.78	12.89	12.39
36	F(Y)	14.17	14.14	13.50	16.05	15.14
T7						
37	F(Z)	13.72	14.19	14.79	15.36	16.13
38	F(Z)	10.20	12.04	11.62	12.84	14.16
39	F(Z)	13.89	14.16	14.69	13.57	12.74
T8						
14	F(X)	15.17	16.63	14.97	14.76	14.61
	F(Z)	0.12	0.05	0.32	0.21	0.26
	F(T)	15.29	16.68	15.29	14.97	14.87
15	F(X)	11.71	11.20	10.96	10.81	11.01
	F(Z)	0.01	0.01	0.01	0.00	0.06
	F(T)	11.72	11.21	10.97	10.81	11.07
16	F(X)	14.82	13.46	12.39	12.10	12.00
	F(Z)	1.31	0.97	1.24	1.25	1.14
	F(T)	16.13	14.43	13.63	13.35	13.14

APPENDIX E
CARCASE DISSECTION PROCEDURE

The techniques described are based on those issued by the Meat and Livestock Commission (1975).

E.1 Entire Carcase Measurements

1. Cold dead weight was recorded.

2. Chest width (mm) was measured at the greatest width using a caliper gauge whilst the carcase was still hanging freely.

3. F (mm) was measured using a steel rule from the most distal point on the medial edge of the central and fourth tarsals to the most caudal point on the median line between the legs.

4. T (mm) was measured from the most distal anterior edge of the central and fourth tarsal bones to the proximal edge of the tibial tuberosity, found by inserting a skewer into the joint between the tibia and femur,i.e into the intercondyloid fossa of the femur.

5. The carcase was sawn down through the centre of the vertebral column. Pieces of spinal cord, large pieces of aorta and diaphragm were removed. The tail was removed to the level of the posterior edge of the 5th sacral vertebra.

6. The weight of the left and right sides were recorded.

E.2 Left side Measurements

1. The maximum depth of the side was measured using a caliper gauge.

2. The length of the side from the anterior edge of the symphysis pubis to the dorsal anterior edge of the first thoracic vertebra was measured using a steel tape measure.

3. Probe measurements of the depth of the subcutaneous fat and M.longissimus dorsi were atken at 4cm from the midline at the level of the centre of the body of the 12th thoracic vertebra.

E.3 Jointing

1.Kidney knob and channel fat ((perirenal fat) was removed as one. The posterior edge of the channel fat in the pelvic cavity was defined by a line running along the posterior border of the sacrosciatic ligament. The kidney was removed. The kidney, kidney knob and channel fat were weighed.

2. Breast and leg joints were obtained by placing pins on the anterior edge of the 12th rib at the most ventral point of attachment with the diaphragm and in the intercondyloid fossa of the femur. With the side hanging , the two pins were joined by a line on the lateral surface. With the side lying on the bench, the leg was marked to the level of the line marked previously, by drawing a line between the ventral posterior edge of the 1st caudal vertebra and a point on the pelvic bone one fifth of the distance between the ventral posterior edge of the last lumbar vertebra and the anterior edge of the symphysis pubis. With the side hanging and the knife held at right angles to the lateral surface a cut was made from the anterior edge of the 12th rib caudally until the line of the leg was met. With the side lying the leg was removed. The anterior part of the breast up to the rib level with the centre of the 6th thoracic vertebra was marked by drawing a line from the point on the 12th rib first marked to the anterior ventral junction of the bone and the cartilage on the 1st rib. After removing, weighing and recording any thoracic fat adhering to the inside of the thoracic cavity, the breast on the fore, from the rib level with the centre of the 6th thoracic vertebra forward, was removed by cutting from the medial surface and at right angles to it from the posterior edge of the costochondral junction of the rib level with the centre of the 6th thoracic vertebra to the anterior dorsal edge of the 2nd sternebra.

3. The chump was removed by a cut at right angles to the long axis of the last lumbar vertebra between the penultimate and last lumbar vertebrae.

4. The loin was separated from the best end of neck by marking the centre of the 12th thoracic vertebra and, with knife held at right angles to the medial cut surface of the vertebral bodies and spine and at right angles to the long axis of the 12th thoracic vertebra, sawing and cutting until the posterior edge of the rib was hit, and then following the curve of the rib until the line of the breast was met. The loin was then divided into two by a cut through the centre of the 3rd lumbar vertebra with the knife held at right angles to its long axis and at right angles to the medial cut surface of the ventral bodies and spine.

5. The best end was separated from the rest of the fore by cutting and sawing through the centre of the 6th thoracic vertebra, with the knife held at right angles to the medial cut surface of the vertebral bodies and spine and parallel to the cut at the level of the 12th thoracic vertebra. Caliper measurements were taken of the depth of subcutaneous fat and subcutaneous fat + M.longissimus dorsi at 3.5cm from the midline on the exposed posterior face of the best end.

6. The neck was removed from the shoulder and middle neck by sawing and cutting along the anterior ventral edge of the 4th cervical vertebra with the knife at right angles to the medial surface of this vertebra and at right angles to its long axis.

7. The shoulder and middle neck were separated by starting on the anterior medial face of M.scalenus ventralis and, working laterally, on to the first rib, finding the natural separation in fat between the shoulder muscles and M.serratus ventralis. M.trapezius was left on the shoulder but M.rhomboideus and M.serratus ventralis remained on the middle neck.

E.4 Full Tissue Separation

Each joint was separated by knife into muscle, subcutaneous fat, intermuscular fat, bone and waste.

Muscle included periosteum (where this came away easliy from the bone), small blood vessels, connective tissue sheaths and small quantities of fat that were physically difficult to separate.

Subcutaneous fat was the external fat down to the level of the connective tissue over the peripheral muscle layer, excluding M.cutaneus muscle which lies in the subcutaneous fat. In the case of the hind and fore legs, the fat under the external connective tissue sheath down to the level of the connective tissue adhering to the peripheral muscles was classed as subcutaneous.

Intermuscular fat was that lying between the muscles, together with thin connective tissues, small blood vessels and small quantities of muscle that were physically difficult to separate.

Bone included cartilage together with small quantities of muscle, fat and other tissues that were difficult to separate. Vertebral bone, including the sacrum, was weighed separately to other bone. The weight and length of the femur (measured from the proximal tip of the trochanter major to the distal edge of the medial condyle) and the weight and length of the tibia/fibula (measured from the most distal point of the fossa between the medial and lateral condyles to the most distal point of the medial malleolus) were also recorded.

Waste consisted of all glands (cleaned of fat), blood vessels (which could be separated easily from the tissue) and tendons. Tendons of the lower leg muscles were cut off at right angles to the line of the tendon at the most distal part of the muscle belly. The ligamentum nuchae was include in this category.

APPENDIX F
CHEMICAL AND ANATOMICAL DATA -- EXP.4

The design of the experiment is given in Tables 3.3 and 3.4. All weights are in kilogrammes.

CHEMICAL DATA

N = lamb identity, pooled pairs are shown together.
LW = liveweight at slaughter; tim = time to slaughter in days; FI = total feed intake to slaughter.
P = protein; Wa = water (excluding loss from warm carcase); A = ash and L = lipid in the shorn empty body.

N	LW	tim	P	Wa	A	L	FI
INIT							
1617	11.7	0	1.81	7.08	0.41	0.84	0
1606	13.0	0	1.97	7.71	0.44	0.91	0
1387	15.9	0	2.31	9.07	0.47	1.59	0
1538	16.9	0	2.52	9.76	0.54	1.82	0
1525	18.9	0	2.76	10.60	0.50	2.17	0
1317	25.0	0	4.03	14.33	0.69	3.02	0
ALHP							
28	31.4	39	4.08	15.12	0.90	2.83	42.77
51	29.8	46	3.84	14.77	0.88	2.78	41.35
35	41.3	71	5.08	19.23	0.86	7.05	92.67
7	48.2	132	5.18	19.49	1.15	12.13	171.00
31	49.1	132	5.24	19.84	1.17	12.40	183.49
24	52.3	132	5.35	19.98	1.15	13.56	173.79
49	61.6	158	6.65	25.16	1.39	16.39	238.63
ALLP							
18	31.5	44	3.77	14.66	0.78	2.92	38.54
60	30.7	46	3.84	14.92	0.81	3.03	35.39
20	53.7	158	5.80	21.87	1.22	13.74	195.14
55	53.9	158	6.02	22.70	1.27	14.27	217.11
70	47.6	158	5.41	20.21	0.97	10.37	188.36

N	LW	tim	P	Wa	A	L	FI
1.2HP							
59	26.8	29	3.34	13.03	0.59	2.52	25.35
39	25.2	25	3.46	13.62	0.60	2.59	16.20
48	30.6	35	3.89	15.30	0.72	3.43	31.26
14	30.2	50	4.04	15.12	0.75	3.54	40.60
68	35.2	71	4.40	16.25	0.98	4.60	67.07
54	34.8	73	4.27	16.25	0.94	4.40	70.61
64	39.3	66	4.40	16.66	0.75	5.69	69.98
22	40.1	109	5.02	18.62	0.86	6.63	100.71
5	44.2	132	5.17	18.56	1.24	8.27	141.81
27	41.1	132	4.64	16.62	1.12	7.47	137.53
16	55.3	144	6.48	19.84	1.86	13.05	199.66
40	52.4	144	6.63	20.08	1.89	13.26	194.28
1.2LP							
10	24.9	29	3.44	12.79	0.75	2.20	20.34
41	24.8	23	3.25	12.53	0.70	2.07	15.19
1	30.6	50	3.78	14.82	0.80	3.28	32.45
50	31.5	50	3.95	15.51	0.84	3.42	42.49
3	35.5	64	4.10	16.08	0.78	3.94	57.66
21	35.3	78	4.22	17.28	0.79	4.00	80.98
12	40.8	106	4.93	18.25	1.01	6.89	102.96
73	40.8	114	4.92	17.98	1.01	6.86	112.14
46	43.2	132	4.52	17.99	1.44	7.83	133.02
52	42.6	132	4.58	18.05	1.47	7.96	137.68
13	49.3	185	5.70	22.40	1.77	11.29	196.54
19	52.7	185	5.99	21.29	1.55	13.99	200.36
34	52.4	185	6.05	21.58	1.52	13.81	200.82

N	LW	tim	P	Wa	A	L	FI
0.8HP							
43	25.3	39	3.23	12.07	0.75	1.95	24.46
58	25.5	53	3.17	11.85	0.72	1.88	24.85
36	30.4	53	3.77	14.28	0.81	2.71	33.96
47	30.4	73	3.55	13.55	0.75	2.51	48.16
56	32.0	135	3.59	13.79	0.67	4.77	100.34
71	33.2	135	3.62	13.58	0.68	4.84	93.47
33	35.6	106	4.34	15.61	0.99	5.45	81.26
62	36.7	176	4.55	16.11	1.08	5.91	125.73
45	41.2	193	4.75	16.79	1.40	6.58	147.80
61	40.8	196	5.03	17.51	1.49	7.04	149.82
Four lambs were not chemically analysed.							
Only their LW, tim and FI data are given:							
65	42.8	273					218.9
42	43.7	273					211.0
25	43.9	273					207.9
26	48.6	273					215.2
0.8LP							
29	24.9	25	2.98	11.89	0.57	2.09	10.17
23	25.4	66	3.18	12.69	0.61	2.25	43.07
57	30.7	73	3.58	13.91	0.67	3.34	47.21
32	29.9	81	3.56	13.84	0.67	2.84	58.08
17	34.8	73	4.20	15.75	0.79	4.12	53.67
44	36.1	114	4.53	16.49	0.87	4.56	81.08
38	38.5	193	4.61	16.47	1.23	6.36	143.17
63	39.2	193	5.08	18.22	1.47	6.61	145.66
66	40.5	193	4.95	17.67	1.42	6.36	142.17
53	41.7	199	5.12	17.92	1.40	6.90	147.76
9	42.8	199	5.48	18.57	1.50	7.37	151.84

ANATOMICAL DATA

FPO = feed processing organs (stomachs + intestines + liver); RO = respiratory organs (heart + lungs); PELT = shorn skin; WOOL = unwashed fleece; BLOD = blood; GFIL = gut-fill

N	FPO	RO	PELT	WOOL	HEAD	FEET	BLOD	GFIL
INIT								
1617	1.30	0.36	0.96	0.21	0.96	0.34	0.56	1.32
1606	1.32	0.40	0.94	0.22	1.00	0.44	0.68	1.46
1387	1.42	0.54	1.40	0.46	1.32	0.46	0.90	1.62
1538	1.42	0.52	1.38	0.34	1.34	0.48	0.66	1.88
1525	1.76	0.54	1.44	0.31	1.36	0.54	1.06	2.30
1317	2.00	0.68	1.90	0.53	1.70	0.78	1.26	2.08
ALHP								
28	3.36	0.78	2.26	0.92	1.74	0.72	1.34	5.28
51	2.80	0.72	2.20	0.64	1.86	0.74	1.22	4.92
35	3.62	0.78	2.84	1.44	2.00	0.96	1.80	6.46
2	3.21	0.92	3.12	1.67	1.98	0.82	1.80	4.52
7	3.83	1.07	3.82	1.70	2.24	1.04	2.06	6.36
31	2.90	1.00	4.82	1.66	2.04	1.04	1.98	6.66
24	2.96	1.04	3.38	1.73	2.18	1.00	2.04	8.46
49	4.18	1.08	4.94	3.33	2.88	1.18	2.76	6.24
ALLP								
18	3.08	0.70	1.84	0.78	1.68	0.72	1.40	7.72
60	2.82	0.66	2.24	0.61	1.58	0.62	1.22	3.62
20	3.71	1.01	3.74	2.60	2.52	1.00	2.28	6.72
30	3.58	1.04	4.08	1.73	2.20	1.00	2.22	4.52
55	3.56	1.05	4.42	2.34	2.38	1.02	2.50	5.10
70	3.17	1.00	4.28	3.17	2.34	0.96	2.14	4.34
1.2HP								
59	2.22	0.66	1.84	0.58	1.52	0.60	0.98	6.16
39	2.44	0.62	1.88	0.51	1.56	0.58	1.16	4.36
48	3.00	0.70	2.14	0.78	1.74	0.68	1.38	5.08
14	2.60	0.69	2.12	0.77	1.54	0.58	1.10	5.82
68	2.84	0.72	2.68	1.15	1.74	0.90	1.48	6.94
54	2.96	0.80	2.52	1.13	1.60	0.74	1.66	6.41
64	2.78	0.70	2.76	1.33	2.06	0.86	1.60	8.24
22	2.85	0.70	2.72	1.23	1.96	0.80	1.72	6.86
5	2.76	0.86	3.70	1.86	2.20	0.98	2.10	6.68
27	2.52	0.89	3.46	1.64	1.86	0.84	1.68	7.76
16	3.65	1.09	3.14	2.41	2.62	0.94	1.98	9.99
40	3.27	1.05	3.62	2.84	2.46	0.96	2.28	6.76

N	FPO	RO	PELT	WOOL	HEAD	FEET	BLOD	GFIL
1.2LP								
10	2.06	0.62	1.84	0.66	1.56	0.58	1.20	4.22
41	2.26	0.62	1.62	0.43	1.54	0.58	1.14	4.94
1	2.54	0.75	2.02	0.69	1.68	0.68	1.52	6.48
50	2.98	0.68	2.18	0.89	1.66	0.68	1.56	6.28
3	3.04	0.74	2.48	0.82	1.70	0.72	1.52	8.42
21	2.85	0.88	2.52	1.08	1.78	0.82	1.84	7.10
12	2.30	0.84	2.92	1.60	1.94	0.80	1.82	7.39
73	2.97	0.82	2.84	1.61	2.16	0.80	1.88	7.66
46	2.98	0.88	3.46	1.60	2.12	0.90	1.84	7.62
52	2.66	0.93	3.36	1.57	2.14	1.11	1.84	6.48
13	3.18	1.12	3.60	1.98	2.12	0.90	2.16	6.04
19	3.23	1.17	3.54	2.36	2.44	0.98	2.08	6.74
34	3.42	0.95	3.70	2.35	2.38	0.94	2.44	6.10
0.8HP								
43	2.18	0.56	1.64	0.75	1.54	0.60	1.02	5.74
58	1.94	0.58	1.88	0.84	1.46	0.52	1.26	6.16
36	2.42	0.70	2.26	0.74	1.66	0.68	1.46	6.88
47	2.54	0.72	2.00	0.87	1.50	0.66	1.52	8.31
33	2.60	0.83	2.60	1.41	1.96	0.82	1.80	6.92
62	2.25	0.80	2.06	1.21	1.92	0.74	1.42	6.76
56	2.48	0.62	2.14	1.30	1.68	0.72	1.56	5.88
71	2.03	0.66	1.96	1.35	1.78	0.86	1.66	4.44
45	2.36	0.78	2.78	2.10	2.04	0.78	1.86	8.58
61	2.45	0.87	2.46	1.38	2.08	0.78	1.82	7.74
26	2.38	1.02	3.98	2.63	2.44	0.96	1.96	7.56
25	2.67	1.08	3.68	0.92	2.64	1.02	2.14	7.10
42	2.74	1.01	3.42	2.17	2.46	0.90	1.74	6.70
65	2.63	0.93	3.38	2.31	2.42	0.92	1.70	7.82
0.8LP								
29	2.48	0.50	2.22	0.60	1.54	0.58	0.86	5.40
23	2.23	0.56	1.88	0.66	1.40	0.58	0.86	4.40
57	2.31	0.64	2.46	1.03	1.68	0.70	1.32	6.64
32	2.31	0.68	2.16	0.99	1.64	0.66	1.30	6.38
17	2.55	0.67	2.80	1.19	1.78	0.80	1.70	7.84
44	2.40	0.83	2.50	1.58	1.76	0.70	1.54	7.15
38	2.50	0.78	2.58	2.06	2.00	0.76	1.98	6.68
63	2.39	0.92	2.86	1.56	2.10	0.82	1.72	5.62
53	2.46	0.86	2.84	2.41	2.30	0.92	1.74	6.80
66	2.66	0.88	2.50	1.64	2.28	0.94	1.96	7.10
9	2.75	0.87	2.90	1.40	2.34	0.90	1.96	8.06

CARCASE DATA

WCAR = warm carcase; CCAR = cold carcase;
MUSC = muscle; TFAT = total dissected fat;
BONE = dissected bone; O+MF = omental and
mesenteric fat.

N	WCAR	CCAR	MUSC	TFAT	BONE	O+MF
INIT						
1617	5.62	5.44	3.36	0.67	1.31	0.16
1606	6.14	5.92	3.63	0.65	1.52	0.14
1387	7.28	7.06	3.87	1.01	1.74	0.18
1538	8.58	8.42	4.34	1.98	1.72	0.26
1525	9.12	8.86	5.28	1.44	1.79	0.24
1317	12.96	12.68	7.19	2.64	2.58	0.54
ALHP						
28	13.34	12.81	7.06	2.48	2.46	0.42
51	13.36	12.81	7.30	2.74	2.11	0.32
35	19.88	19.22	9.87	5.90	2.85	0.78
2	20.84	19.94	8.95	7.91	2.56	1.50
7	23.60	23.22	10.73	8.07	2.80	1.56
31	23.86	23.52	9.06	10.89	2.89	2.18
24	26.74	26.36	11.35	11.21	3.04	2.02
49	30.90	30.18	14.05	13.13	3.71	3.32
ALLP						
18	12.86	12.09	7.09	2.12	2.24	0.38
60	13.20	12.68	6.92	2.93	2.05	0.52
20	26.30	25.78	11.35	10.93	3.05	3.24
30	29.16	28.54	11.66	13.70	2.96	3.24
55	28.40	27.70	11.84	12.16	3.26	1.96
70	21.96	21.42	9.78	8.49	2.72	2.36
1.2HP						
59	11.18	10.83	6.20	1.86	2.23	0.36
39	11.50	11.04	6.40	2.36	1.98	0.34
48	13.92	13.16	7.39	2.49	2.22	0.42
14	13.72	13.38	7.50	3.24	2.18	0.60
68	15.62	15.31	8.74	3.56	2.62	0.52
54	15.22	14.45	7.56	3.90	2.22	0.58
64	16.66	15.97	9.56	3.41	2.70	0.54
22	19.84	19.40	10.56	6.02	2.56	1.00
5	20.90	20.44	11.05	5.74	3.03	1.08
27	18.64	18.28	8.62	6.21	2.86	1.06
16	25.78	25.18	11.26	9.28	3.82	2.16
40	25.90	25.58	11.60	9.27	3.71	2.38

N	WCAR	CCAR	MUSC	TFAT	BONE	O+MF
1.2LP						
10	11.34	10.94	6.62	1.77	1.94	0.32
41	10.74	9.96	5.88	1.85	1.99	0.36
1	13.02	12.66	7.25	2.58	2.29	0.36
50	13.34	12.98	7.50	2.66	2.06	0.40
3	14.48	14.18	8.18	3.26	2.33	0.48
21	15.40	14.39	8.20	3.47	2.36	0.56
12	18.88	18.18	9.69	5.52	2.50	1.16
73	18.76	18.28	9.20	5.32	2.61	0.76
46	19.84	19.36	9.11	7.10	2.40	1.06
52	20.40	19.98	10.66	6.46	2.49	1.12
13	25.20	24.90	11.79	9.35	3.36	1.94
19	27.76	27.18	13.77	9.85	3.13	1.90
34	26.02	25.46	11.47	10.73	2.85	3.50
0.8HP						
43	10.52	10.07	6.09	1.21	2.04	0.26
58	10.12	9.68	6.06	1.59	1.83	0.22
36	12.50	11.95	7.12	2.53	2.08	0.26
47	11.46	10.86	6.25	2.18	1.86	0.27
33	15.58	14.94	7.72	3.79	2.76	0.58
62	17.58	17.00	8.07	5.44	2.71	1.26
56	14.28	13.30	6.66	3.90	2.27	0.60
71	14.80	14.08	7.57	3.73	2.30	0.46
45	18.50	17.94	9.22	5.01	2.89	0.80
61	19.82	19.46	10.13	5.67	2.92	1.08
65	19.46	19.12	10.25	5.50	3.00	0.96
42	21.44	21.11	11.61	6.33	2.91	1.18
25	21.72	21.33	11.82	5.93	3.37	0.82
26	23.24	22.87	12.46	6.94	3.21	1.26
0.8LP						
29	10.12	9.56	5.75	1.26	2.14	0.26
23	11.28	10.62	6.29	2.09	1.89	0.36
57	12.66	11.99	6.55	2.86	2.04	0.42
32	12.84	12.09	6.83	2.89	1.99	0.54
17	14.30	13.56	7.82	2.89	2.31	0.54
44	16.26	15.80	8.55	3.69	2.41	0.66
38	17.04	16.40	8.21	4.40	2.57	1.28
63	19.46	18.92	10.08	6.14	2.77	1.22
53	19.58	19.00	9.55	5.71	2.98	1.02
66	18.46	18.08	9.80	4.16	3.27	0.68
9	20.50	20.08	10.99	5.59	3.19	1.08

APPENDIX G
ANATOMICAL DATA -- EXP.5

The experimental design is given in Table 4.3. All weights are in kilogrammes. N = identity, t = time from 25kgLW to slaughter, GF = gut-fill, PLUC = lungs+heart, LIVE = liver, CFAT = caul fat.

N	t	LW	GF	HEAD	PELT	FEET	PLUC	LIVE	GUTS	CFAT
UR										
1649	0	25.5	3.06	1.46	1.97	0.69	0.70	0.42	2.14	0.14
1643	0	24.5	2.69	1.46	2.08	0.62	0.69	0.41	1.96	0.12
1964	0	24.5	2.98	1.32	2.22	0.56	0.72	0.38	1.72	0.24
1955	0	26.5	3.20	1.48	2.20	0.64	0.84	0.43	1.90	0.30
1904	0	24.5	4.21	1.61	2.00	0.60	0.56	0.42	1.99	0.08
1141	0	25.5	5.41	1.42	1.90	0.55	0.64	0.46	2.34	0.33
2329	37	35.5	6.08	1.64	3.30	0.73	1.00	0.78	3.02	0.24
1979	33	36.0	6.70	1.72	2.80	0.73	1.02	0.68	2.90	0.38
1978	37	35.0	4.50	1.72	2.60	0.76	0.74	0.58	2.10	0.50
1128	42	39.5	6.02	1.88	3.66	0.86	0.98	0.74	2.08	1.22
1695	56	40.0	7.08	1.86	3.50	0.74	0.96	0.86	2.82	1.12
1981	57	42.0	5.26	1.94	3.67	0.92	0.93	0.64	2.44	0.80
1932	70	44.5	5.92	2.08	4.42	0.98	0.92	0.71	2.68	0.94
1619	76	46.0	5.42	2.04	4.47	0.80	0.90	0.98	2.68	1.20
1644	79	45.5	7.90	2.48	4.61	0.84	0.90	0.76	3.10	0.78
R										
1038	0	24.5	6.40	1.34	1.88	0.54	0.50	0.42	1.74	0.10
1627	0	24.5	4.95	1.25	2.28	0.50	0.61	0.40	1.83	0.14
1612	0	26.5	5.03	1.32	2.53	0.62	0.54	0.51	1.82	0.10
1925	0	25.5	4.14	1.52	2.51	0.62	0.58	0.48	1.58	0.18
2308	0	25.5	3.46	1.72	3.03	0.60	0.50	0.42	2.34	0.56
2358	0	25.0	3.78	1.38	2.02	0.58	0.52	0.46	1.70	0.10
1139	57	36.0	4.52	2.14	3.64	0.81	0.84	0.80	2.42	1.43
2307	45	35.5	3.90	2.14	3.94	0.78	0.86	0.66	2.58	0.55
2569	50	34.5	6.30	2.10	3.47	0.70	0.92	0.90	3.20	0.50
2338	51	40.5	4.56	2.04	3.86	0.80	1.02	0.80	2.70	0.72
1041	77	42.0	5.70	2.08	4.71	0.74	0.98	0.80	2.80	1.60
1617	58	40.5	4.60	2.40	4.66	1.14	1.02	0.78	2.10	1.08
2306	91	46.5	4.86	2.08	4.40	0.94	1.14	0.90	2.04	1.60
2352	94	46.0	6.68	2.24	5.30	0.86	0.94	0.80	2.22	1.88
1567	77	45.0	5.88	2.36	4.91	0.90	1.17	1.03	3.23	1.22

CARCASE DATA

CARC = cold carcase, MUSC = muscle, SCF = subcutaneous fat, IMF = intermuscular fat, KKCF = kidney knob and channel fat, TFAT = total fat.

N	CARC	MUSC	SCF	IMF	KKCF	TFAT	BONE
UR							
1649	10.94	6.18	0.80	1.04	0.13	1.97	2.15
1643	9.89	5.44	0.59	1.04	0.14	1.77	2.00
1964	10.37	5.47	1.06	1.26	0.24	2.56	1.76
1955	12.21	6.80	1.19	1.37	0.28	2.83	2.03
1904	10.51	6.48	0.71	1.20	1.11	2.02	1.85
1141	10.73	5.88	0.97	1.52	0.21	2.70	1.96
2329	15.59	7.86	1.84	2.01	0.25	4.11	2.65
1979	15.25	7.73	1.55	2.21	0.35	4.11	2.51
1978	14.50	7.95	1.93	1.79	0.28	4.00	2.19
1128	17.38	8.54	2.95	2.36	0.45	5.76	2.62
1695	17.88	8.54	3.04	2.74	0.52	6.30	2.54
1981	18.40	8.94	2.93	2.80	0.60	6.33	2.74
1932	19.91	9.35	3.30	3.15	0.60	7.06	2.89
1619	21.24	9.73	4.61	3.10	0.63	8.34	2.73
1644	21.18	10.29	3.50	3.30	0.63	7.43	2.95
R							
1038	8.26	5.04	0.37	0.73	0.08	1.18	1.78
1627	8.18	4.53	0.51	0.81	0.13	1.44	1.83
1612	8.98	5.55	0.39	0.86	0.11	1.36	1.76
1925	10.13	5.50	1.06	1.36	0.21	2.63	1.69
2308	10.02	5.80	0.79	0.89	0.13	1.81	1.96
2358	9.11	5.01	0.77	0.99	0.17	1.93	1.57
1139	16.95	8.58	2.31	2.44	0.44	5.19	2.65
2307	15.52	8.23	1.94	2.10	0.39	4.43	2.47
2569	16.41	8.23	2.17	2.44	0.49	5.11	2.61
2338	19.48	8.94	3.50	3.19	0.91	7.60	2.45
1041	21.53	9.45	4.64	3.61	0.82	9.07	2.58
1617	19.10	9.73	2.67	2.87	0.45	5.99	2.83
2306	23.25	10.04	4.58	3.78	1.71	10.07	2.39
2352	22.49	9.24	4.21	4.20	1.24	9.64	3.00
1567	20.69	8.38	3.53	3.74	0.94	8.21	3.23